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UNIVERSITY OF NEBRASKA COLLEGE OF AGRICULTURE
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This research bulletin is the result of cooperative investigations conducted by the Department of Agronomy of the Nebraska Agricultural Experiment Station, where Melvin D. Jones was formerly a graduate assistant. Cooperating in the work was the Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils and Agricultural Engineering of the U. S. Department of Agriculture. L. C. Newell is agronomist with the Division, detailed to the Nebraska Station. Melvin D. Jones is now assistant professor of plant breeding and genetics, Oklahoma Agricultural and Mechanical College.

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Pollination Cycles and Pollen Dispersal in Relation to Grass Improvement

MELVIN D. JONES AND L. C. NEWELL

THE plant breeder is initially concerned with gaining a knowledge of the breeding behavior of his plant materials in order that improvement may be undertaken effectively. It is important to know the different characteristic pollination habits of these plants. To develop and apply techniques applicable to the improvement of a given grass crop, it is desirable to know the time of day and the number of days that the grass sheds pollen. The effects of temperature, humidity, light, and wind on pollination must be considered.

Once superiority of germ plasm is obtained, the most important consideration is the maintenance of this genetic identity with the advance in generation of these selected plant materials. The problem of maintaining genetic identity differs with self-fertilized and cross-pollinated plants. Procedures and requirements set up for use in the production and maintenance of superior varieties or strains of cross-pollinated grasses must be based on facts regarding the wind dissemination of their pollen. In spite of the interest in this subject, there has been reported in the literature little experimental evidence upon which proper distances for field isolation may be based.

The primary objectives of these investigations were to determine the time of day and the number of days that certain grasses shed pollen, and to determine the relative amounts of pollen of selected grasses dispersed in the air at various distances from their sources.

Part I - - Pollination Cycles

INVESTIGATIONS were conducted at Lincoln, Nebraska, during 1944 and 1945 to determine some of the characteristic pollination habits of various grasses. Studies were made of several grasses to determine the length of time during the day when pollen was present in the air, the number of days on which pollen was shed, and the day of maximum pollen shedding. This information was desired in order to know when adequate quantities of pollen could be obtained so as to facilitate the development of hybridization techniques applicable to an improvement program with these grasses. The effects of temperature, light, humidity, and wind on anthesis and pollen shedding were considered. Bromegrass, crested wheatgrass, western wheatgrass, intermediate wheatgrass, tall fescue, Kentucky bluegrass, rye, buffalograss, blue grama, switchgrass, and corn received more attention than other grasses.

Historical Review

HILDEBRAND (9), Godron (8), and Fruwirth (7) have observed most thoroughly the phenomena of pollination in grasses. Knuth (13) reviews the accounts of Hildebrand, Kerner, Kirchner, Warnstorff, and Beyerinck, but not those of Godron or Fruwirth, and gives a discussion of the conditions of pollination. Other investigators (7, 13, 21, 23) have described in detail the process of blooming in grasses. According to Vinall and others (22), regardless of the type of grass inflorescence, blooming begins near the apex of the inflorescence and progresses more or less regularly toward the base. In the spikelet the reverse is true; the basal florets open first, followed in regular order by those above.

Godron (8) has more accurately defined certain factors which influence blooming. He found, in observations made during three years, that the temperature particularly influenced the time of day of blooming. If temperature is lower than that required as a minimum for complete blooming, there are fewer florets blooming; if it is considerably lower, blooming is delayed for several hours, or even until another day. Fog and heavy dew delay the hour of blooming, as does also moistening of the buds by rain just before blooming time. Shading delays the time of blooming, while dryness particularly accelerates dehiscence of the anther. A cloudy sky, providing there is sufficient heat, has no noticeable influence.

Fruwirth (7) reports that not only do the weather conditions of a day exercise a great influence on the time of appearance of the first blooming and of the most frequent blooming of that day, but the conditions of the previous day exercise a similar influence. The latter may, by retarding the blooming, provide more florets that are ready for anthesis the following day.

As a result of experiments conducted on the effect of artificial light on pollination, Fruwirth (7) concludes that lack of light greatly reduces rather than prevents blooming of grass florets. If there is sufficient heat and light, blooming is only somewhat delayed. Stephens and Quinby (21) found that by placing sorghum plants in a dark room during the day and exposing them to artificial light at night, the natural rhythm of blooming was reversed in 36 hours. They concluded that light conditions are a most important factor in governing the time of blooming.

Several investigators have studied the effects of humidity on the time of blooming. Sando (18) and Stephens and Quinby (21) state that humidity does not influence the time of blooming. Leighty and Sando (14) observed wheat flowers to open without dehiscence of the anthers when placed in water. However, Fruwirth (7) and Godron (8) state that humidity delays the time of blooming.

Stephens and Quinby (21) state that in the absence of wind to disturb the sorghum panicle, blooming was retarded for an undetermined period of time. When florets had not begun to open after the usual time for heavy blooming, vigorous agitation of the panicle or stalk produced an abundance of open florets within 30 minutes.

Under field conditions, blooming was observed to occur twice during the day by Beddows (2) in *Bromus arvensis* L.; by Sando (18) in *Agropyron elongatum* (Host) Beauv., and by Fruwirth (7) in *Arrhenatherum elatius* (L.) Presl, *Phleum pratense* L., and *Dactylis glomerata* L.

Experimental Procedure and Results

FROM OBSERVATIONS that were made on many grasses, it was found that when meteorological conditions were favorable, blooming occurred daily at a rather regular time for each grass studied in its particular season. This phenomenon of daily regularity of blooming and pollen shedding is designated as a *daily pollination cycle* throughout this investigation.

It was found that a succession of blooming of florets within a spikelet, and of blooming of florets in different spikelets within an inflorescence constitutes a *seasonal pollination cycle* which lasts several days for a single inflorescence. The seasonal pollination cycle for a variable population of plants would be extended in time over that of a single inflorescence. This would result because of the blooming of a succession of florets on different tillers of a plant and from variable plants in a grass field. These inherent variations in time of blooming and pollen shedding of a plant population account in part for the daily amount of pollen shed.

In addition, environmental factors may affect the daily amount of pollen shed and the number of days of blooming and pollen shedding. As will be shown later in this investigation, temperature appeared to produce the most decisive effects on blooming and pollination cycles in grasses.

Studies on the time of day and number of days of pollen shedding were conducted near Lincoln, Nebraska, in forage grass fields isolated from other fields of the same species. These fields were breeding blocks of spaced plants or small fields grown in solid stands for seed increase. Fields sown to rye and fields of corn checked in 42-inch rows were used in studying these cereal crops.

In order to determine the time of day and the number of days a grass sheds its pollen, microscope slides which had an area of one square inch coated with a thin film of vaseline were exposed at two elevations near the height of the plant in the center of the selected grass field. The slides were placed in holders that were attached to weather vanes at an angle of 45°. This method of exposure kept the vaseline-coated side of the slide exposed against the prevailing wind and facilitated catching the pollen that was impinged against the slide, whether it was blown through the air or fell as a result of gravity. The total number of pollen grains on 10 random low-power microscope fields (16 sq. mm. area) per slide was used throughout this investigation as a measure of the amount of pollen shed.

Where it was not possible to obtain complete isolation of the grass under study, the nearby field or roadsides were mowed prior to blooming. Volunteer plants of the same or different species which might cause contamination on slides were rogued prior to pollen shedding.

Grass pollen is easily identified from the pollen of other families of plants, dust particles, and rust spores, which were the chief contaminants. No key for the identification of grass pollen has been published; however, several aids were used in determining the kinds of pollen encountered. Knowledge of which kinds of plants were shedding pollen at the same time of the year, and the time of day that each kind of plant sheds its pollen were important considerations. Size and shape measurements as well as the mass effect of the pollen under study made intruder pollen of different sizes or shapes conspicuous.

Time of Day of Pollen Shedding

Close observation of the anthers previous to blooming made it possible to predict when pollen shedding might be initiated by a given grass. For these studies, preliminary exposures were made every three to four hours during the first days when the investigation of a grass was begun. After the general time of day when pollen was being shed from the anthers was determined, intensive studies were continued from two to six days. Exposures were made at 30-minute intervals during the period of active pollen shedding. When microscope examination revealed no pollen was being caught on the slides, the 30-minute time exposures were discontinued. Slides were left exposed until the following day, when the more frequent exposures were started again. Counts of pollen from these slides constituted the record of pollen shedding for each 24-hour period, as well as for periods of several days. The counts made at 30-minute intervals were recorded on the basis of central standard time.

Cool-Season Grasses

For practical discussion, grasses have been classified in recent years into two general groups on the basis of seasonal growth habits: the cool-season and the warm-season grasses. The cool-season grasses begin to grow in early spring, making their maximum vegetative growth during the early, cool months of the growing season. Frequently, they also make a vigorous growth during the fall months. Because of the earliness of spring growth, this group furnishes the first grasses of the season to come into anthesis and to produce seed. Of this group, the grasses studied included bromegrass, crested wheatgrass, western wheatgrass, intermediate wheatgrass, tall fescue, Kentucky bluegrass, and the annual cereal—common rye.

Bromegrass. Of the cool-season group, bromegrass, *Bromus inermis* Leyss., proved to be one of the most interesting in its blooming and pollen-shedding habits. Observations made on these phenomena during typical days of pollination disclosed that occasional plants started anthesis by 3:00 p.m. The number of plants that were blooming continued to increase very slowly until 4:30 p.m. At this time, the slender, yellow anthers had been extruded from the glumes on most of the plants in the field. The majority of the plants began anthesis in the 15-minute period from 4:25 p.m. to 4:40 p.m. On the average, it required only 15 minutes after blooming until the anthers started dehiscing and shedding pollen. Under humid conditions, more time was required. In a few minutes after maximum blooming, "clouds" of pollen were observed as breezes swept across the field. These observations have been substantiated by data obtained from slides exposed for 30-minute periods, during this part of the day, throughout the seasonal pollination cycle.

The number of pollen grains counted on the slides as an average of six days during the 1945 season was low until 4:30 p.m., when 150 were recorded (Fig. 1). After the next 30-minute period an average of 250 were counted, and by 5:30 p.m. the peak of 330 pollen grains per 30-minute exposure were obtained. The number fell to 113 for the period 5:30 to 6:00 p.m., and to only 15 pollen grains for the next 30-minute period. No pollen was caught on slides left exposed from 7:00 p.m. until 2:00 p.m. the following day. The majority of the pollen grains was shed from 4:00 until 6:00 p.m., a period of only two hours, the peak being reached at 5:30.

Data obtained from daily counts showed that pollen shedding was delayed 30 minutes to one hour on afternoons following days of heavy pollen shedding. On these days fewer florets were ready to open in the earlier part of the day, and only a small number matured during the day, which probably accounts for the pollen shedding being light and the peak being reached later in the day. The peak of pollen shedding occurred at 5:30 p.m. on June 17, 19, and 21, while it was delayed until 6:30 p.m. on June 18 and until 6:00 p.m. on June 20.

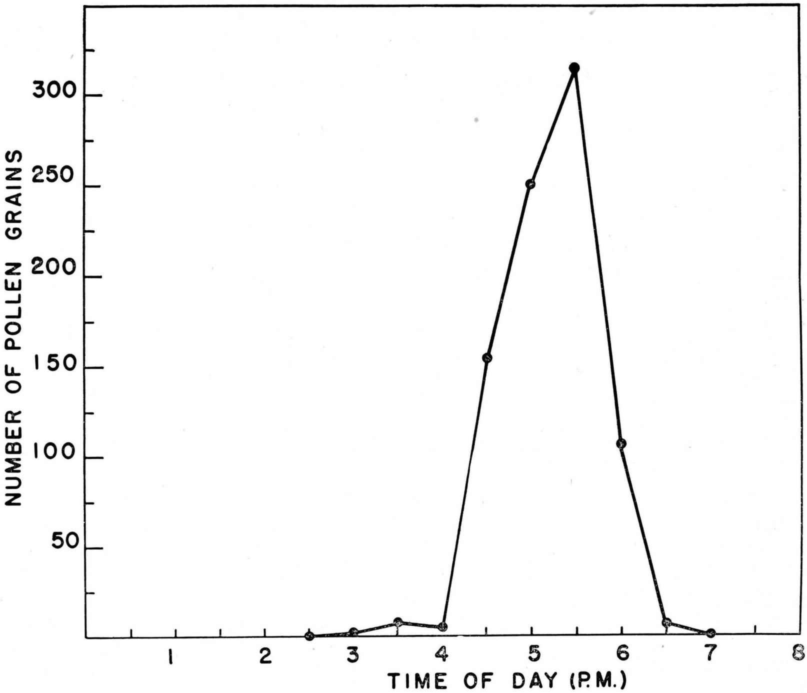

Fig. 1. The number of pollen grains caught on 16 sq. mm. areas of microscope slides exposed in the center of a bromegrass field during 30-minute periods of the day. Average for six days in 1945.

On June 22, the heaviest pollen shedding of the season occurred, the peak being reached at 4:30 p.m. This very heavy shedding, which occurred one hour earlier in the day than average, may be partially explained by the fact that a 48-hour period had elapsed since the previous heavy shedding. During this time a large number of anthers had reached maturity, which probably caused a larger relative number of florets to bloom early in the day. This response resulted in the peak of pollen shedding occurring a short time earlier than average.

During this six-day period, conditions of temperature, humidity, and light were extremely favorable to pollen shedding. Temperatures of 80° to 85° F. were found to be optimum for the blooming of this grass; however, active blooming has been observed to take place at temperatures between 74° and 90° F. The average daily peak did not occur until 5:30 p.m., although readings made at 30-minute intervals showed that temperatures were favorable during the entire afternoon. Temperatures lower than 70° F. inhibited blooming on June 14 and 15, 1945.

Under field conditions, bromegrass was never observed to bloom more than once in a given day; however, in the greenhouse, where temperatures could be carefully regulated, it was possible to make it bloom twice during the day. During the pollination period, a temperature of approximately 60° F. was maintained in the greenhouse during the night and early morning. No blooming occurred at this temperature. The ventilators were closed at 8:30 a.m. and the temperature immediately rose to 85° to 90° F. By 9:30 a.m. the plants had started blooming, and a heavy uniform pollen shedding continued for approximately one hour, which resulted in an abundance of pollen. The ventilators were opened again at 10:30 a.m., and the greenhouse cooled to 65° F. This temperature was maintained until 3:00 p.m., when the same procedure was repeated; however, the blooming was relatively light the second time.

Sporadic blooming and pollen shedding of bromegrass plants under greenhouse conditions has usually resulted in poor seed setting. By using temperature controls of pollination and thereby assuring a maximum of pollen at the time most of the blooming occurs, excellent seed production has been obtained which in some instances has surpassed that obtained under field conditions.

Wheatgrasses. Studies of pollination cycles were conducted with three wheatgrass species. Crested wheatgrass, *Agropyron cristatum* (L.) Beauv., was studied for a period of four days in 1945. Western wheatgrass, *Agropyron smithii* Rydb., was studied for two days in 1945. Intermediate wheatgrass, *Agropyron intermedium* (Host) Beauv., was studied for two days in 1944 and also in 1945. Because of the similarity of the

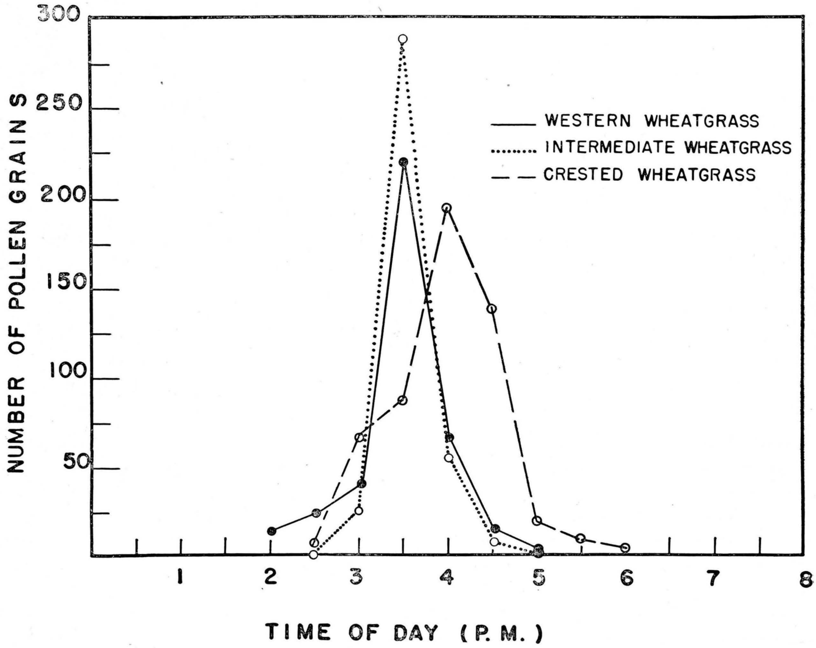

Fig. 2. The number of pollen grains caught on 16 sq. mm. areas of microscope slides exposed in the center of wheatgrass fields during 30-minute periods of the day. Average of pollen counts from two days for intermediate wheatgrass and western wheatgrass and four days for crested wheatgrass in 1945.

time of blooming and pollen shedding, the data for these grasses are presented and discussed together.

By observing typical days of pollen shedding in 1945, it was found that a few anthers were extruded from the glumes between 2:30 and 3:00 p.m., but the majority of them appeared between 3:00 and 3:15 p.m. in western wheatgrass and intermediate wheatgrass, and between 3:30 and 3:45 p.m. in crested wheatgrass. Dehiscence of the anthers and pollen shedding took place approximately 20 minutes after blooming. The data on intermediate wheatgrass for 1944 showed that the average peak of pollen shedding occurred at 4:00 p.m., and in 1945 at 3:30 p.m. The average for each grass in 1945, shown in Figure 2, indicates that maximum shedding occurred at 3:30 p.m. for western wheatgrass and intermediate wheatgrass, and at 4:00 for crested wheatgrass. Small amounts of pollen were shed until 6:00 p.m. Slides exposed at 6:00 p.m. and left until 1:00 p.m. the following day were free of pollen. The period of active pollen shedding varied from one and one-half to two hours.

Data for individual days can be selected for each of these grasses which show practically identical blooming and pollen-shedding phenomena as far as time of day is concerned. The data obtained for these species of *Agropyron,* as well as observations made on grasses of the *Bouteloua* and *Andropogon* genera, indicate that under similar meteorological conditions blooming tends to take place at approximately the same time of day for closely related species which have evolved under the same general environmental conditions.

The optimum temperatures required for blooming and pollination of the wheatgrasses appears to be between 80° and 85° F. These grasses apparently are not as sensitive to low temperatures as is bromegrass, since they bloomed and shed pollen somewhat earlier in the day. However, temperatures on most days were favorable several hours before the blooming in the wheatgrasses occurred.

Kentucky Bluegrass. The daily pollination cycle of Kentucky bluegrass, *Poa pratensis* L., occurs at low temperatures and much of it during darkness. Slides that were exposed at 9:00 p.m. and left during the night showed a pollen count representing approximately 87 per cent of the daily amount of pollen shed. Blooming and pollen shedding were observed at a temperature of 51° F. This temperature was the lowest at which these phenomena were observed in any species investigated during the two-year period. The fact that the genus *Poa* originated in a very cold climate may explain this result.

Tall Fescue. Data obtained from slides exposed for periods of 30 minutes in a field of tall fescue, *Festuca elatior* L. var. *arundinacea* (Schreb.) Wimm., indicate that a few plants began blooming by 1:00 p.m. each day; however, the majority of the plants bloomed shortly before 2:00 p.m. Based on an average of three days' data in 1945, maximum pollen shedding occurred at 2:30 p.m. (Fig. 3). The most active period was from 1:30 until 3:30 p.m., with a small number of pollen grains being caught on each exposure until 5:30 p.m. Slides that were exposed from 5:30 p.m. until 11:00 a.m. the following day had only an occasional pollen grain on them. Tall fescue compared favorably with bromegrass in the rapidity with which the anthers burst forth from the glumes and the period of 25 minutes required for the anthers to dehisce and shed pollen. Blooming took place actively at temperatures of

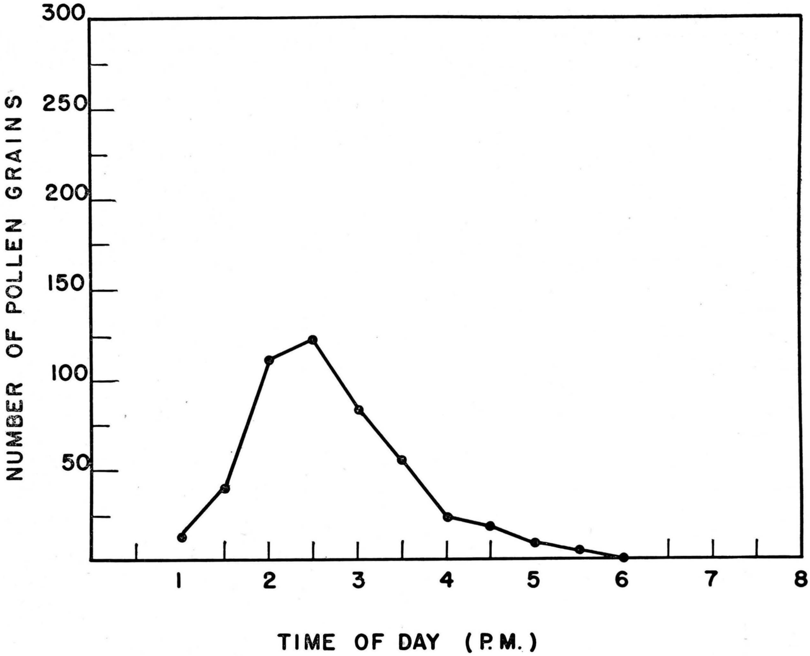

Fig. 3. The number of pollen grains caught on 16 sq. mm. areas of slides exposed in the center of a tall fescue field during 30-minute periods of the day. Average counts for three days in 1945.

65° to 85° F. with 78° F. being optimum. Light bloomings were observed to occur at temperatures from 58° to 60° F. Where slides were exposed over 24-hour periods for a week, there were days of heavy and moderate pollen shedding in this species, similar to those described for bromegrass. As was the case with bromegrass and the wheatgrasses, temperatures were favorable for three to five hours on most of the days before blooming occurred.

Rye. With rye, *Secale cereale* L., as well as with Kentucky bluegrass, it was necessary to begin exposures of slides before dawn to determine the extent of pollen shedding. As observed in 1945, the daily pollination cycle occurred during the morning hours. Blooming and pollen shedding continued slowly from 2:30 until 6:30 a.m. The anthers required approximately 50 minutes to dehisce. After blooming was completed, a slight agitation of the plants caused small clouds of pollen to fall. Slides were placed on the ground so that the number of pollen grains which fell to the ground could be compared with the number caught on the slides exposed in the air at elevations of 2.5, 5.0, and 10.0 feet. Almost four times as many pollen grains were caught on the ground exposures as on any of the other three. This indicates that most of the pollen being shed fell directly to the ground under these conditions.

During 30-minute periods on May 26 when light breezes swept across the field a large number of pollen grains were caught on the slides. Only a small number were caught during periods of calm. Considerable variation is accordingly shown in the number of pollen grains caught during different 30-minute intervals (Fig. 4).

A wind velocity of seven mph. on May 29 resulted in the pollen being dispersed immediately upon dehiscence of the anthers. The rate of pollen shedding for 30-minute periods increased from 20 pollen grains for the period from 2:30 to 3:00 a.m. to a maximum of 350 for the period from 6:00 to 6:30 a.m. After the peak was reached, a rapid decline in number of pollen grains followed until 8:30 a.m. Only a small number of pollen grains were caught on the exposures made between 8:30 and 11:00 a.m. Slides that were exposed from 11:00 a.m. until 9:00 p.m. were free of pollen. The number of pollen grains caught on the ground exposures on May 29 were approximately equal to the highest number caught on any of the slides exposed at greater elevations. The two daily records of pollen shedding (Fig. 4) indicate that wind is important in regulating the uniformity with which pollen is dispersed into the air in large quantities for pollination under natural conditions.

The minimum temperature at which rye was observed to bloom was 57° F. on May 23, 1945. Temperatures from 70° to 85° F. appeared to be optimum; however, rye bloomed under a variety of temperature conditions. The blooming and pollen shedding of the annual cereal crops

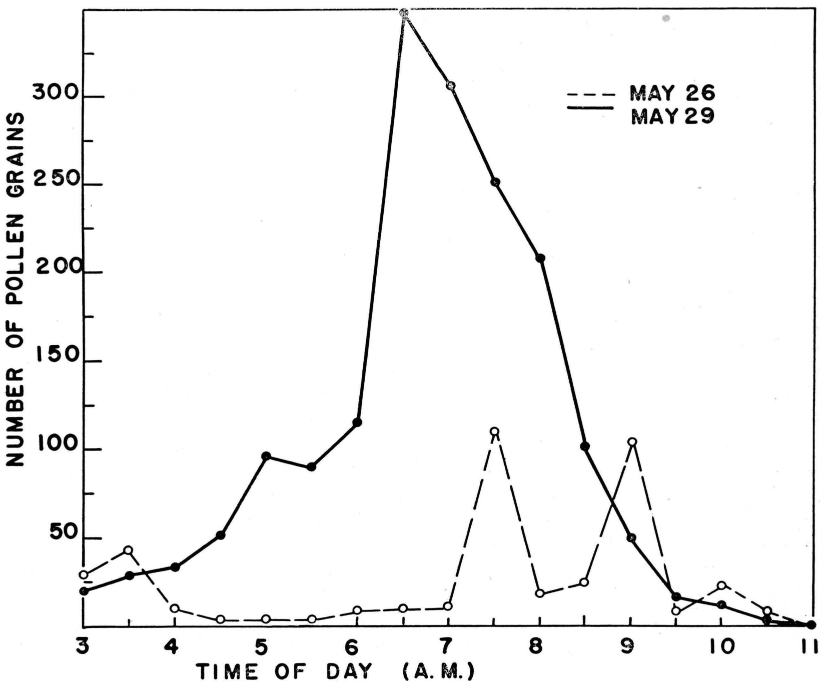

Fig. 4. The number of pollen grains caught on 16 sq. mm. areas of slides exposed in the center of a rye field, during 30-minute periods of the day, on May 26 and 29, 1945.

and Kentucky bluegrass during the morning hours constitute pollination characteristics different from those exhibited by the other cool-season perennial grasses as determined in this study. These differences appear to be due largely to different responses to temperature.

Warm-Season Grasses

The warm-season grasses as a group begin growth somewhat later in the spring than the cool-season grasses, with maximum growth being produced during the warm months of the year. The time of occurrence of anthesis and seed production varies from relatively early to late in the growing season. Of the grasses studied, buffalograss and the gramas appear to be least determinate in flowering as to day length and temperature. Buffalograss begins anthesis early in the growing season, and the gramas often produce two crops of seed, while the bluestems and switchgrass are long-season crops, usually utilizing most of the growing season before the completion of a seed crop. This group accordingly furnished material for studies of pollination phenomena throughout the season.

Buffalograss. Observations on the blooming and pollen-shedding habits of buffalograss, *Buchloë dactyloides* (Nutt.) Engelm., were made during the 1945 season. It was found that by 6:30 a.m. a few anthers were visible, and by 7:00 a.m. a uniform blooming of the plants had occurred. Approximately 30 minutes were required for the anthers to dehisce. Since the spikes were only six to ten inches from the ground, relative humidity was high—a condition which retards dehiscence and pollen

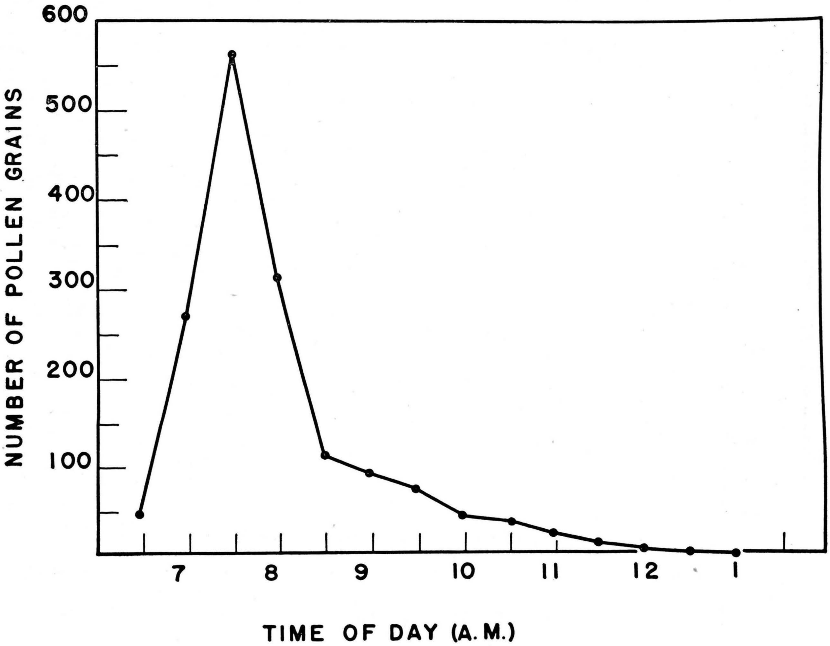

Fig. 5. The number of pollen grains of buffalograss caught on 16 sq. mm. areas of slides exposed in the center of the field. Readings made during 30-minute periods of the day. Average counts on two days in 1945.

shedding. Based on two days' data obtained from exposed slides, it was shown that the most active period of pollen shedding lasted from 7:00 until 8:30 a.m. with the peak at 7:30. From 8:30 a.m. until 1:00 p.m. a gradual decline occurred in the number of pollen grains shed (Fig. 5).

On another day of light showers and high relative humidity, blooming was only slightly delayed, but no pollen was shed until after 9:30 a.m., a delay of approximately three hours due to high humidity.

A temperature range from 70° to 80° F. appears to be optimum for blooming; however, light blooming was observed at 59° F. on May 23, 1945. Blooming in buffalograss is not retarded as much by low temperatures as it is in the other warm-season grasses investigated.

Blue Grama. Preliminary studies with blue grama, *Bouteloua gracilis*, (H.B.K.) Lag., had shown that it was necessary to begin exposures before daylight to determine the time of day of pollen dispersal. In observing typical days of pollination, it was found that a few anthers were extruded from the glumes by 3:00 a.m.; however, full bloom did not occur until 4:15 a.m. Approximately 35 minutes were required for the anthers to dehisce and pollen shedding to start. The data obtained from slides exposed for 30-minute periods during three days indicate that the most active period of pollen shedding occurred from 4:50 until 5:50 a.m., a period of only one hour, with the maximum occurring at 5:00 (Fig. 6). From 6:00 until 9:00 a.m., a decreasing number of pollen grains con-

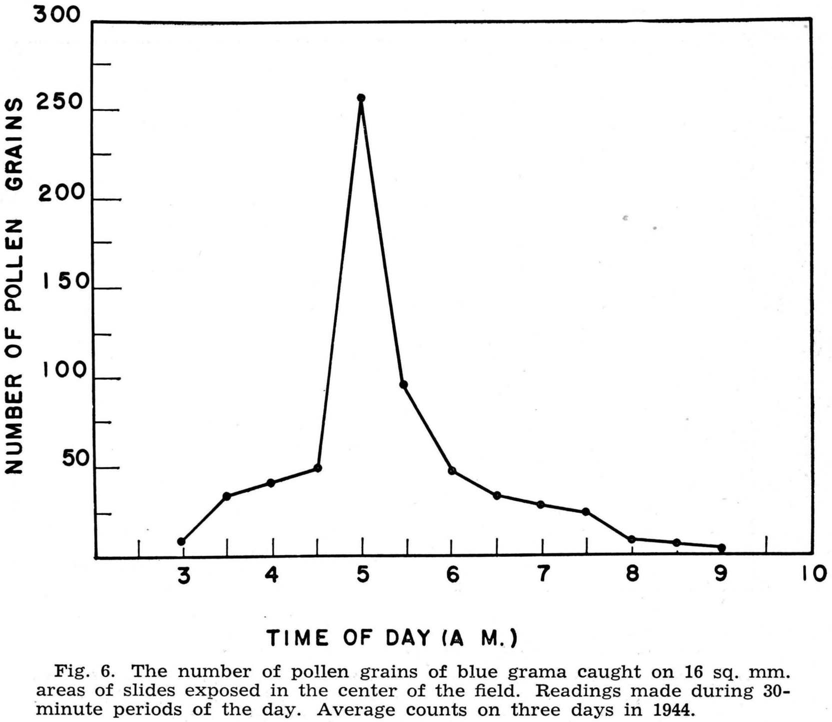

Fig. 6. The number of pollen grains of blue grama caught on 16 sq. mm. areas of slides exposed in the center of the field. Readings made during 30-minute periods of the day. Average counts on three days in 1944.

tinued to be shed. After 9:00 a.m. no pollen was shed until the following morning.

The active period of blooming and pollen shedding took place in darkness, under a temperature of 65° F. and a relative humidity of 55 per cent. Low temperatures appeared to be responsible for the long period of an hour and 45 minutes of most active blooming.

On the third morning of study, a light shower fell at 4:10 a.m., 20 minutes before the plants came into full bloom. Blooming was not noticeably delayed by the moisture, but dehiscence of the anthers and pollen shedding were delayed until 8:30 a.m., at which time the relative humidity had dropped to 65 per cent. Very little wind movement was observed, and only a small number of pollen grains were caught on the slides during the day. A temperature of 60° F. inhibited blooming and pollen shedding in this strain of blue grama on September 16, 1944.

Switchgrass. In 1944, occasional plants in a field of switchgrass, *Panicum virgatum* L., were observed to start blooming by 10:00 a.m., with the majority blooming shortly before 10:30 a.m. Within 10 minutes after the florets opened, the anthers had dehisced and were shedding pollen. The peak of shedding occurred at 11:00 a.m.; however, the most active period extended from 10:30 until 12:00 noon. (Fig. 7). This peak of pollen shedding occurred later in the morning than in any other of the warm-season grasses studied. Three or four pollen grains per 30-minute period continued to be caught on the slides until 2:30 p.m. Slides left

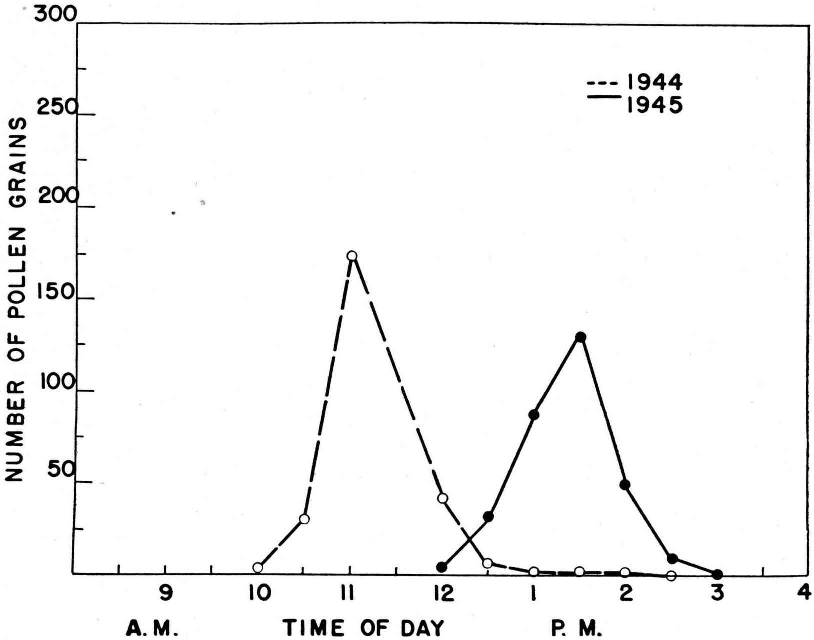

Fig. 7. The number of pollen grains caught on 16 sq. mm. areas of slides exposed in the center of a switchgrass field during 30-minute periods of the day. Average counts for two days in 1944, and three days in 1945.

exposed from 3:00 p.m. until 9:00 a.m. the following morning were free of pollen.

In August, 1945, light blooming was observed by 12:00 noon, and it continued until 1:00 p.m. when the maximum bloom was reached. Within 20 minutes after the florets opened, the anthers had dehisced and were shedding pollen. The peak of pollen shedding occurred at 1.30 p.m., with the most active period extending from 12:30 until 2:00 p.m. Exposures that were made at 3:00 p.m. and left until the following morning were free of pollen (Fig. 7).

In 1944 active blooming and pollen shedding occurred under conditions of low relative humidity and a temperature of 93° F. Temperatures lower than 72° F. inhibited blooming of switchgrass in the greenhouse on January 10, 1944.

On August 17 and 18, 1945, active blooming was observed to occur at 11:00 a.m. under temperatures of 83° and 87° respectively. Temperatures of 70° and 75° F., respectively, were the lowest recorded during the nights preceding these days of blooming. These observations compare favorably with the results obtained in 1944. From August 22 to 26, temperatures ranging from 52° to 58° F. were recorded at 7:00 a.m. Slides were exposed at intervals of 30 minutes on August 24, 25, and 26. The average peak of pollen shedding for these days occurred at 1:30 p.m. The low night temperatures, which were below the apparent minimum for blooming in switchgrass, delayed blooming and pollen shedding approximately 2.5 hours. A combination of a low temperature during the night and early morning (58° F. at 6:00 a.m.) and a low temperature in late morning (66° F. at 11:00 a.m.) delayed maximum blooming and pollen shedding until 2.30 p.m. on August 25.

Switchgrass was the only warm-season grass that was observed to bloom in the afternoon. It appears that temperatures below the minimum for blooming in any of the warm-season grasses may result in delaying their blooming until afternoon. The low night temperatures that occur in the early spring when the cool-season grasses are coming into anthesis may account for the fact that many of these grasses bloom and shed pollen in the afternoon.

Corn. Observations of pollination in corn (*Zea mays* L.) made on two days in 1944 showed that scattered plants in a corn field began blooming at 7:40 a.m., with the maximum bloom reached at 8:30 a.m. The period of most active pollen shedding extended from 8:30 until 11:00 a.m., with the peak being reached at 9:30 (Fig. 8). A small number of pollen grains continued to be dispersed in the field until 4:00 p.m. Slides left exposed from 5:00 p.m. until 6:00 a.m. the following morning were free of pollen.

A similar study was conducted with corn for three days in 1945 (Fig. 8). Blooming and pollen shedding occurred approximately 30 minutes earlier in the day than in 1944. The most active period of shedding extended from 7:30 until 11:00 a.m. with the maximum being reached at 9:00. A decreasing number of pollen grains was caught during 30-minute periods until 4:00 p.m. (Fig. 8).

Pollinating bags were placed over tassels at 1:00 p.m. and again at 3:00 p.m. on days of heavy pollen shedding, but only a few pollen grains could be obtained by vigorously agitating the tassel. Most of the pollen was shed between 8:30 and 11:00 in the morning, and the pollen grains that were caught on slides exposed in the afternoon were probably pollen

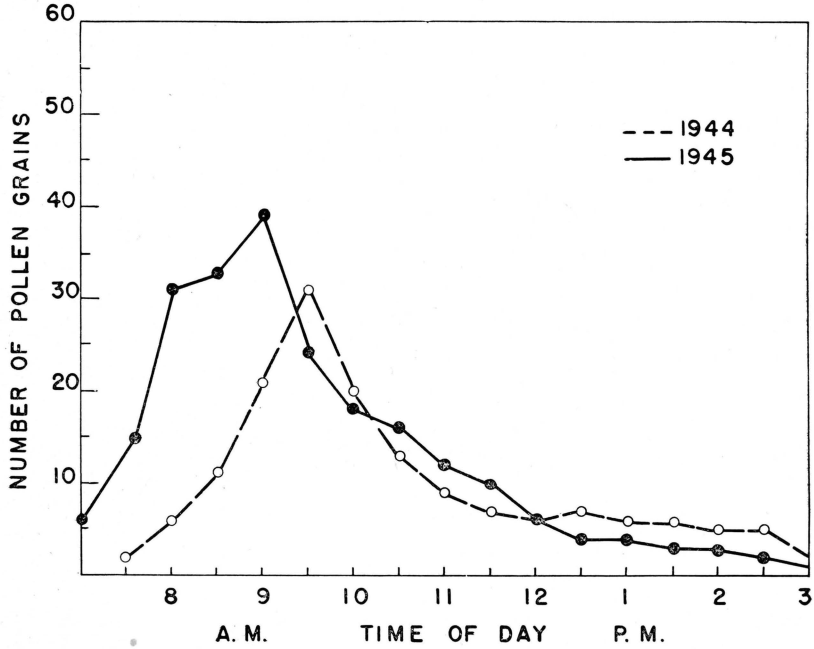

Fig. 8. The number of pollen grains caught on 16 sq. mm. areas of slides exposed in the center of a corn field during 30-minute periods of the day. Average for two days in 1944, and three days in 1945.

grains that had lodged on leaves and that upon disturbance were later dispersed into the air.

The peak of pollen shedding for different days occurred at temperatures ranging from 72° to 91° F. A temperature of 65° F. on August 23, 1945, delayed blooming for three hours.

Number of Days of Pollen Dispersal

For these studies, microscope slides were exposed for a period of 24 hours. Exposures were begun one or two days previous to the initial day of pollen shedding, and daily exposures were continued throughout the seasonal pollination cycle.

The number of days that a grass sheds pollen is increased where the plant material is genetically heterogeneous. Uniform soil moisture and fertility and uniformity of plant type shorten the seasonal pollination cycle.

Wolfe (23) working with orchard grass found that it required an average of 6.7 days for all the flowers on a single head to bloom, and 13.5 days for all the flowers on a single plant to bloom. Evans (5) found that the flowers on a single spike of timothy bloomed for six to sixteen days. Leighty and Sando (14) found that blooming continued from four to five days in wheat. From his observations on 13 grasses, Fruwirth (7) reported that on the average a single inflorescence blooms from four to six days. *Alopecurus pratensis* L., which required three to four days, and *Arrhenatherum elatius,* which required seven to eight days, were the extremes. Stephens and Quinby (21), working in Texas, found that most varieties of sorghums bloomed from eight to ten days with the maximum blooming being reached on the third or fourth day. Some late varieties bloomed for 15 days. According to Kiesselbach (12), as an average for the two years 1914 and 1915, the duration of pollen shedding by individual corn plants was six days.

Bromegrass. Records of bromegrass pollination at Lincoln, Nebraska, for the period 1936 to 1943 show the seasonal pollination cycles to have occurred in late May or early June. In 1944, under conditions where temperatures ranged from 55° to 65° F., accompanied by high humidity, pollination did not occur until June 11. Many anthers had grown to maturity during this period, but none had shed pollen.

On June 11, 1944, bright sunlight and optimum temperatures (75° to 85° F.) prevailed throughout the day. The heaviest pollen shedding observed during the two-year period occurred between 1:00 and 2:00 p.m., which was the earliest time in the day that this phenomenon had been observed in bromegrass at Lincoln. This early pollination may be ascribed not only to the conditions of that particular day, but also to the accumulation of fully matured florets during the previously unfavorable conditions. This first day was the day of maximum pollen shedding during the 1944 pollination season. Data obtained from exposed slides showed 4,164 pollen grains were caught per 16 sq. mm. area (Fig. 9).

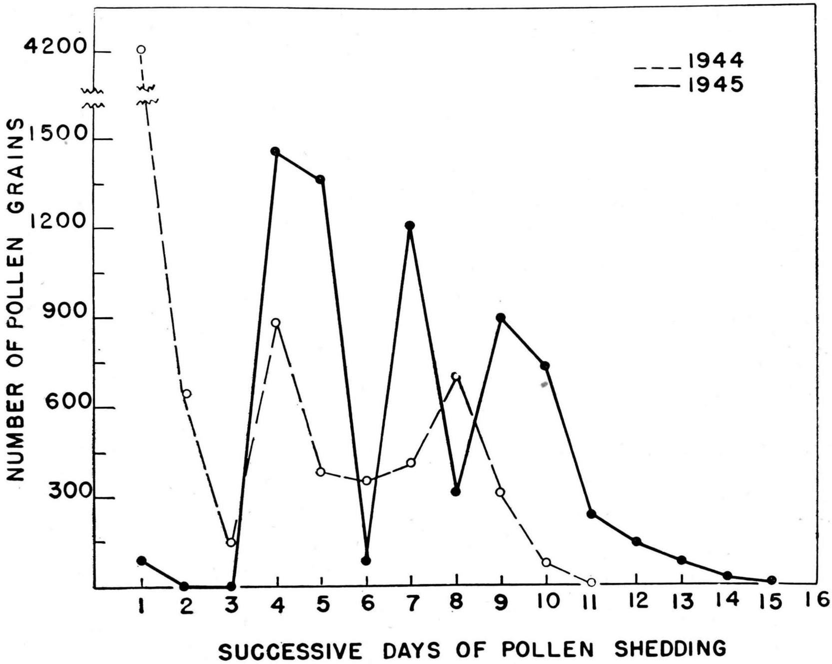

Fig. 9. The number of pollen grains caught on 16 sq. mm. areas of microscope slides exposed on successive days in the center of a bromegrass field during pollination in 1944 and in 1945.

(This number is the equivalent of 166,560 per sq. inch or 23,984,640 per sq. foot.)

During the succeeding days, pollen shedding occurred in late afternoon as has been shown to be typical (Fig. 1). On the second day only 643 pollen grains were caught on the same area per slide, and this number diminished to 149 pollen grains on the third day. Moderate pollen shedding occurred on the fourth and eighth days, followed in each case by three days of light pollen production.

During the first day of pollination in 1945 only 90 pollen grains were caught per unit of slide area. On the second and third days, temperatures of 60° and 69° F. inhibited pollination (Fig. 9). Heavy pollen shedding occurred on the fourth, fifth, seventh, ninth, and tenth days. For one or more days after each peak a light pollen shedding occurred.

As an average for 1944 and 1945, in a bromegrass breeding nursery, pollen shedding extended over a period of twelve days, while in a field planted to a selection of uniform type the pollen shedding lasted for only eight days.

Kentucky Bluegrass. Daily exposures of slides were made in a field of Kentucky bluegrass during the 1945 pollination season. Only three pollen grains per 16 sq. mm. area were caught on the first day of pollination.

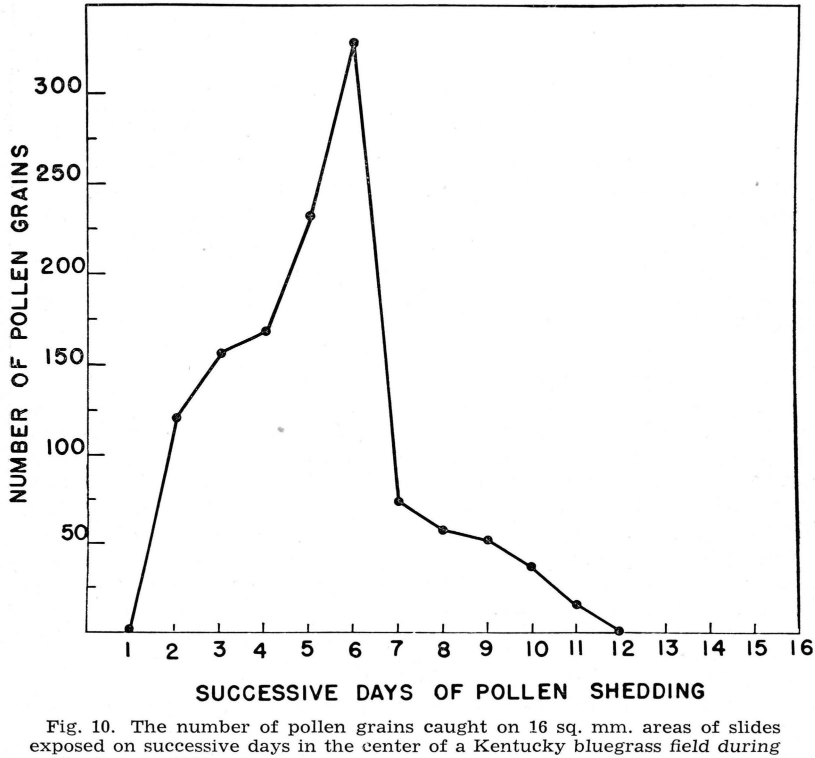

Fig. 10. The number of pollen grains caught on 16 sq. mm. areas of slides exposed on successive days in the center of a Kentucky bluegrass *field during* pollination in 1945.

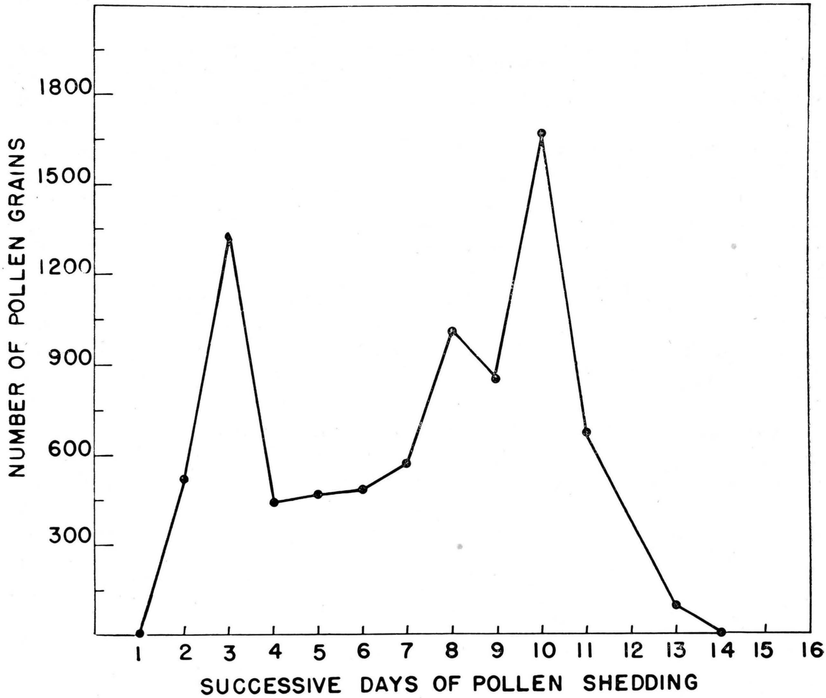

Fig. 11. Number of pollen grains caught on 16 sq. mm. areas of slides exposed on successive days in the center of a rye field during pollination in 1945.

A gradual daily increase continued until the sixth day when 327 pollen grains were counted. A sudden decline occurred on the seventh day, and continued until the twelfth day when pollen shedding ceased entirely (Fig. 10). Pollen dispersal in Kentucky bluegrass was affected less by low temperatures than in any other species studied. This may account for the daily regularity with which pollen was shed.

Rye. The number of days of pollen shedding in rye was determined during the 1945 pollination season. A gradual daily increase occurred, reaching 1,328 pollen grains per unit of slide area on the third day. Six days of moderate shedding followed until the maximum was reached on the tenth day. A rapid decline in number of pollen grains shed continued until pollen shedding ceased on the fourteenth day (Fig. 11).

Corn. The daily amount of corn pollen shed per inflorescence during the seasonal pollination cycle was measured during 1944.* Experiments were conducted twice during the season with F_1 hybrids selected for study. Ten tassels that were beginning to shed pollen were tagged each day for 11 consecutive days. During the afternoon of the eleventh day, a pollinating bag was placed over each tassel. The following morning pollen was shaken from the tassels into the bags and weights were taken. Plants that

* The authors are indebted for assistance and cooperation in this particular study to Mr. John H. Lonnquist, Assistant Agronomist, in charge of the corn breeding program at the Nebraska Agricultural Experiment Station.

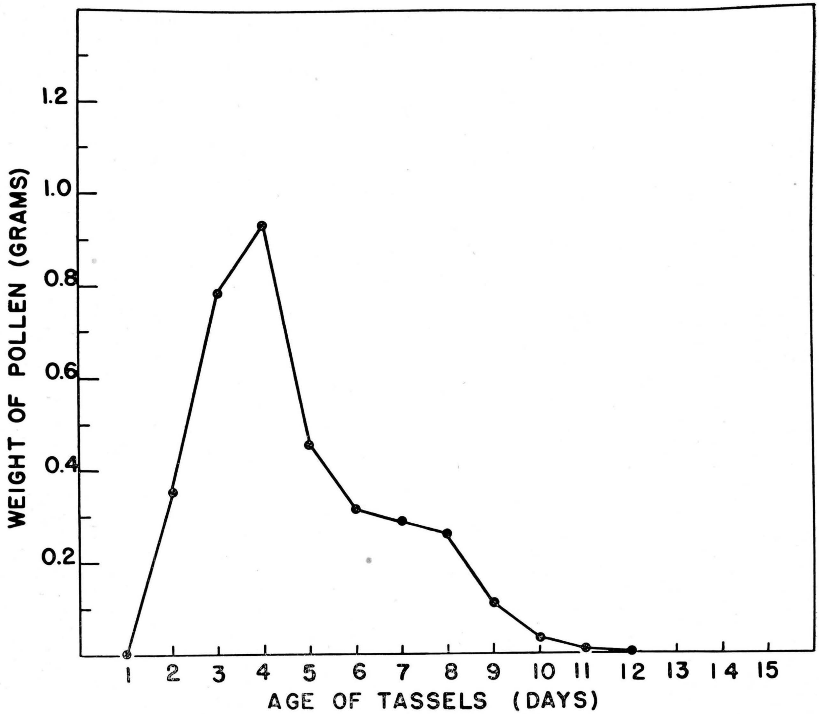

Fig. 12. The average amount of corn pollen shed by tassels of different ages during pollination in 1944.

were tagged the first day of the experiment had been shedding pollen for 12 days. Similarly, plants that were tagged on the second and third days had been shedding pollen for 11 and 10 days, respectively. Since the tassels were tagged on the first day anthers appeared, the number of days a tassel had been shedding pollen was moved up one, i.e., one day after tagging was actually the second day of shedding for a given tassel.

The amount of pollen shed increased until 0.93 gram per tassel was obtained from tassels which had been shedding pollen for four days. Smaller amounts were obtained on tassels of greater ages until no pollen was caught from tassels 12 days old (Fig. 12).

A study of individual corn tassels indicated that spikelets near the apex of the long spike-like racemes, which constitute the panicles, bloom first and blooming continues downward toward the base. However, in the individual spikelets, the basal florets bloomed one to three days ahead of the upper florets. These same blooming phenomena were observed in most of the grass studied.

Observations on Other Grasses

During the 1944 and 1945 seasons, a total of 16 cool-season grasses and 13 warm-season grasses were studied to determine the number of days and the time of day in which pollen shedding took place. In this group

Table 1. Duration of pollen dispersal period and time of day of blooming and pollen shedding of 29 grasses as observed during 1944 and 1945.

Species	Average pollen dispersal period (days) per inflorescence	Time of day of blooming and pollen shedding
Cool-season grasses:		
Agropyron cristatum (L.) Gaertn.	8	2–6 p.m.*
" elongatum (Host) Beauv.	7	2–6 p.m.
" intermedium (Host) Beauv.	10	2–6 p.m.*
" repens (L.) Beauv.	7	2–6 p.m.
" smithii Rydb.	7	2–6 p.m.*
Alopecurus carolinianus Walt.	4	5–8 p.m.
Arrhenatherum elatius (L.) Presl.	7	3–7 p.m.
Bromus inermis Leyss.	10	2–7 p.m.*
Elymus junceus Fisch.	7	3–7 p.m.
Festuca elatior L.	7	3–8 p.m.
" ovina L.	6	4–8 p.m.
" elatior var. arundinacea (Schreb.) Wimm.	9	1–6 p.m.*
Koeleria cristata (L.) Pers.	7	3–7 p.m.
Phleum pratense L.	10	4–9 a.m.
Poa pratensis L.	8	3–8 a.m.*
Secale cereale L.	8	3–11 a.m.*
Warm-season grasses:		
Andropogon furcatus Muhl.	7	4–7 a.m.*
" halli Hack.	8	4–9 a.m.
Bouteloua gracilis (H.B.K.) Lag.	6	3–9 a.m.*
" curtipendula (Michx.) Torr.	8	4–9 a.m.*
Buchloë dactyloides (Nutt.) Engelm.	Indeterminate	6–11 a.m.*
Eragrostis trichoides (Nutt.) Wood	7	7–11 a.m.
Panicum virgatum L.	12	10 a.m.—2 p.m.*
Phragmites communis Trin.	10	6–10 a.m.
Sorghastrum nutans (L.) Nash	8	6–10 a.m.
Sorhum vulgare var. sudanense (Piper) Hitchc.	10	6–12 a.m.
Sorghum vulgare Pers.	10	4–10 a.m.
Spartina pectinata Link	10	4–10 a.m.
Zea mays L.	10	7 a.m.—4 p.m.*

* Observations confirmed by data from exposed slides.

of 29 grasses, the 13 investigated by exposures of slides have previously been discussed. Observations were made on 16 other grasses as to the same phenomena. These observations are summarized in Table 1 along with the findings for the grasses studied more intensively.

It should be emphasized that observation alone is not always completely reliable to determine the time of day and the number of days that grasses shed pollen. With some grasses which are not prolific pollen producers, the exposure of slides has proved the inadequacy of casual observation.

The number of days of blooming and pollen dispersal in grass inflorescences appeared to average seven to eight days for most grasses. Blooming continued for only four days in *Alopecurus carolinianus,* while it continued for 12 days in *Panicum virgatum.* These grasses were the extremes. Blooming was indeterminate in *Buchloë dactyliodes.* In this grass, intermittent blooming was observed for one to ten weeks on the same plant where spikes matured at different dates. In grasses with large, open panicles or long spikes, blooming appeared to occur over a greater number of days than in grasses with small spikes. This probably resulted in the period of blooming and pollen shedding being extended over a greater number of days in *Agropyron intermedium, Bromus inermis, Phleum pratense, Phragmites communis, Spartina pectinata, Zea mays, Panicum virgatum,* and the *Sorghums,* than in grasses such as *Bouteloua gracilis* and *Alopecurus carolinianus.* Strain individuality within a grass apparently accounted for some variation in this respect.

Blooming occurred at approximately the same time of day for five species of *Agropyron,* as well as for the closely related *Elymus junceus.* Blooming occurred slightly earlier in *Festuca elatior* var. *arundinacea* than in *F. elatior* and *F. ovina.* The species of *Andropogon* and *Bouteloua* bloomed between 3:00 and 9:00 a.m. In *Sorghum,* three species were observed to bloom between 6:00 a.m. and 12:00 noon.

Of the cool-season group, *Phleum pratense, Poa pratensis,* and *Secale cereale* bloomed and shed pollen in the morning. The other grasses of this group bloomed and shed pollen in the afternoon. All the grasses studied in the warm-season group bloomed and shed pollen in the morning; however, in *Panicum virgatum* and *Zea mays* the shedding of pollen continued from morning until afternoon.

Discussion

WHEN THE METEOROLOGICAL CONDITIONS were optimum for blooming, the daily pollination periods occurred rather regularly at the same time of day for each grass throughout its seasonal pollination cycle. With many of the grasses, it was observed that the external factors were favorable to blooming several hours each day during the seasonal pollination cycle before blooming actually occurred. This would seem to indicate that certain inherent factors were involved which tended to regulate the periodicity of blooming under favorable environmental conditions.

It was found that, when a grass is ready for blooming, certain external factors singly or in combination may inhibit or delay blooming for an extended period of time. It appears that the time of day of blooming of grass florets is the result of the interaction of inherent and external factors.

With the cool-season grasses, in which blooming was observed to occur under high temperatures, it seemed essential to have the full impact of the heat radiated throughout the morning and early afternoon hours to produce enough growth in the anthers for maturation and for blooming to occur in the afternoon of that day. In the warm-season grasses, which bloomed in later summer under favorable temperature conditions throughout the day, blooming occurred in the morning. This appears to be a logical explanation for the blooming phenomena observed in these groups of grasses.

If the above assumptions are true, it would seem possible to predict that grasses such as bromegrass which normally bloom and shed pollen in late afternoon, between 5:00 and 6:00 p.m. at Lincoln, Nebraska, would bloom earlier in the day when grown farther north. There the pollination cycle would begin later in the season and during longer days, allowing a longer period of suitable conditions during the earlier part of the day for growth and maturation of the anthers, and consequent blooming. This hypothesis is supported by observations made by D. C. Smith*

* D. C. Smith, associate professor of agronomy, University of Wisconsin, Madison. Personal correspondence with the senior author, July 10, 1945.

at Pullman, Washington, from 1936 to 1940, where blooming in bromegrass occurred between 11:00 a.m. and 3:30 p.m. Smith later observed the time of day of blooming in bromegrass at Madison, Wisconsin. He states that at Madison in 1942 blooming occurred shortly after 1:30 p.m., with only sporadic anthesis earlier in the day, while in 1943 and 1944 blooming occurred somewhat later in the day with the peak being reached at 4:00 p.m.

From an examination of these observed phenomena, it would also seem probable that the warm-season grasses studied at Lincoln might be expected to bloom and shed pollen somewhat later during the day if they were grown in higher latitudes or altitudes, which would cause the nights to be cooler, thus delaying blooming during the early morning hours until conditions were more favorable.

The description given previously in this paper on the inherent factors which affect pollination cycles would seem to indicate that, in dealing with a population of variable plants under favorable environmental conditions, a gradual daily increase in the amount of pollen shed might be expected to occur until the maximum is reached, and that this would be followed by a daily decrease in amount until pollen shedding ceased. This phenomenon is largely true with the warm-season grasses, such as buffalograss, blue grama, switchgrass, and corn, which shed their pollen during a part of the growing season with usually favorable temperature conditions. With the cool-season Kentucky bluegrass the same relationship was observed; however, this grass is adapted to shedding pollen under lower temperatures than the other grasses studied.

On the other hand, an alternation of days of light and heavy pollen shedding occurs frequently with the cool-season grasses. This alternation is due to variation in daily temperatures during this part of the season. The florets that bloom on a day of low temperatures are few, resulting in light pollen shedding. However, on the following day a greater number of florets have grown to maturity during this delayed period and they are ready for blooming, which results in heavy blooming and pollen shedding during days of favorable conditions.

A knowledge of these blooming and pollen-shedding phenomena is of extreme importance to the grass breeder in the collecting of large quantities of pollen from a given grass and in making hybridizations at the proper time in the field when there is the least danger of contamination by foreign pollen in the air.

Part II - - Pollen Dispersal

THE MAINTENANCE of strain purity in cross-pollinated grasses is dependent on adequate isolation, based primarily on the distance that pollen is dispersed by the wind. For the most part, the isolation requirements used as standards in certified seed production have been based on observation rather than extensive experimentation. This investigation had as its purpose the determination of the amounts of pollen dispersed at various distances from the field, as this is a factor in undesired outcrossing. Some data will also be presented on the viability of pollen subjected to conditions similar to those which pollen would encounter in traveling such distances.

Blackley (3) conducted a series of differential and quantitative tests on the pollen content of the air in England by attaching greased slides to kites. Scheppegrell (19) mapped the distribution of pollen at different elevations in the air by exposing sticky slides. Erdtman (4) states that pollen grains of certain sedges and grasses are carried in great quantities by the wind for more than 625 miles into the middle of the ocean. New techniques for exposing microscope slides from airplanes are being developed as a means of determining the concentration of microorganisms, pollen, and insects in the upper atmosphere (1, 16).

In 1939, Putt (17) exposed sets of eight microscope slides in vertical and horizontal positions at four elevations in sunflower, bromegrass, and crested wheatgrass fields, as a means of comparing the relative amounts of pollen dispersed in the air from these crops.

Standards of isolation for the production of certified seed have been set up by the International Crop Improvement Association from time to time. In its report of December, 1943 (10), standards were given for timothy, bromegrass, orchard grass, meadow fescue, and crested wheatgrass. In order to be eligible for the production of registered or foundation and certified seed, fields of these grasses must be isolated 60 and 25 rods, respectively, from strains of grasses with which they might be cross-pollinated. These distances could be further reduced where suitable barriers or difference in time of maturity exist. In a later publication of this organization, January, 1945 (11), the following tentative recommendations on isolation were submitted.

Classes	Minimum isolation distance required (Rods)	
	Timothy Orchardgrass	Meadow fescue Bromegrass Crested wheatgrass
Foundation	40	60
Registered	20	40
Certified	10	20

In the same report a sliding scale of 40 rods or less, depending on the size of field, number of border rows, natural barriers, etc., is suggested for corn. For sorghum minimum isolation distances of 40 and 60 rods are required for use in the production of certified and foundation seed, respectively.

At a committee meeting of the International Crop Improvement Association in New Brunswick, N. J., on June 4, 1945, the following minimum isolation distances were suggested for the group of grasses including timothy, bromegrass, orchard grass, meadow fescue, and crested wheatgrass: for foundation seed 40 rods, for registered seed 20 rods, and for certified seed 10 rods. These isolation requirements were adopted at the December, 1945, meeting with somewhat greater isolation requirements for certain grasses grown only in the Great Plains states.

According to Pedersen (15) and to the certification standards of the International Crop Improvement Association (10, 11), a greater isolation is required for the production of certified and foundation seed in certain foreign countries than in the United States.

Experimental Procedure and Results

ISOLATED GRASS FIELDS of 1/10 to 1/4 acre were chosen for the dispersal studies. Microscope slides were exposed at elevations of 2.5, 5.0, and 10.0 feet in the manner described in Part I. A point in the field where slides were exposed at these three elevations is designated as a station. In the initial stages of this investigation an ideal field plan was followed in

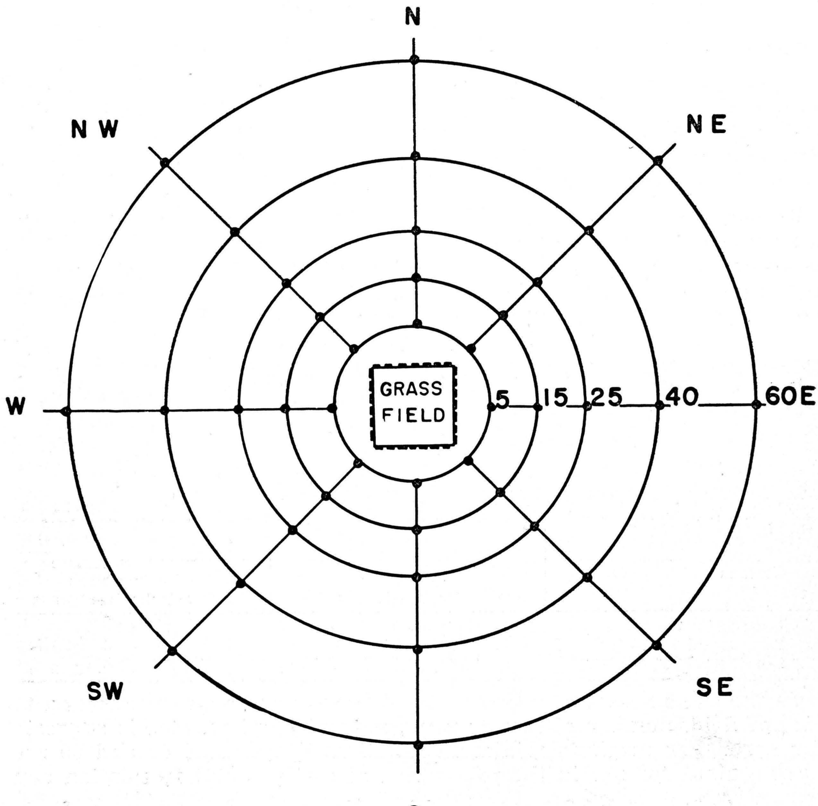

Fig. 13. Location of stations in eight directions about a grass field as used in the initial studies for the determination of pollen dispersal. Numbers indicate distances (rods) from field.

arranging stations about a grass field (Fig. 13). Stations were placed in the center of the field and in each of eight directions at distances of 5, 15, 25, 40 and 60 rods from the field. After some experience had been gained in making exposures, it was found that sufficient data could be obtained during the seasonal pollination cycle without completely surrounding the field. Thereafter, slides were exposed at all stations to the north of the field (opposite the prevailing winds) and only at selected check stations in other directions.

After exposure the slides were collected and labeled as to distance and direction from the field and the elevation at which each was exposed. From the studies conducted on time of day of pollen shedding, it was determined when and for how long each day it was necessary to expose slides in order to catch the pollen. The total number of pollen grains on ten random low-power microscope fields (16 sq. mm. area) on each slide was used as the measure of pollen dispersal throughout the study. A record of the meteorological conditions was obtained by placing an anemometer and a hygrothermograph in the fields during the period of investigation (Fig. 14).

Dispersal of Pollen of Selected Grasses

Investigations were conducted during the 1944 and 1945 pollination seasons to determine the relative pollen load carried by the wind at distances of 5, 15, 25, 40, and 60 rods from the field sources of several grasses. Bromegrass, crested wheatgrass, intermediate wheatgrass, switchgrass, rye, and corn were studied during the two years and buffalograss in 1945.

Bromegrass. A bromegrass field was surrounded by stations in 1944, according to the plan presented in Figure 13. This necessitated a daily exposure of 123 microscope slides. The daily period of pollen shedding in bromegrass extended from 2:30 until 7:00 p.m. (Fig. 1). The slides were exposed before 1:30 p.m. and collected after 8:00 p.m.

Fig. 14. Bromegrass field with equipment used in making studies on the dispersal of pollen.

South winds prevailed throughout the pollination season and the pollen was caught for the most part only on the slides exposed to the north of the field. At a distance of five rods some pollen was caught in each of the eight directions from the field. This was probably due to a swirling of the wind on the south side of the field, resulting in a lateral diffusion or overflow of the pollen in each direction for a short distance.

During the 1944 season, no pollen shedding was observed on days when the wind blew from a northerly direction; however, in 1945 some shedding occurred on warm days accompanied by north winds. It is assumed that pollen would be blown as far with winds from one direction as by winds of similar velocity from another. Because of the experience gained in 1944, slides were exposed at all stations to the north of the field in 1945, and only at the 5 and 15 rod distances to the east, west, and south. Accordingly only the data obtained under the general conditions of southerly winds are presented. Pollen counts are given from those stations to the north of the field and only from stations in other directions when caught in appreciable numbers.

Data taken in 1944 and in 1945 on the day of maximum pollen shedding are presented in Table 2. As a two-year average of three elevations in the center of the field, there were 623 pollen grains caught daily per

Table 2. Number of pollen grains of bromegrass caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field on the day of maximum pollination. South wind 9.5 mph., June 14, 1944. South wind 6 mph., June 22, 1945.

Distance (rods) and direction from the field	1944				1945				2-year av.
	Elevation (ft.)				Elevation (ft.)				Three
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	elevations
Center	453	344	47	281	1520	1244	130	965	623
5 N	230	192	123	182	760	672	471	634	408
NE	17	13	17	16	10	12	13	12	14
NW	12	12	14	13	15	15	14	15	14
Average	86	72	51	70	262	233	166	220	145
W	18	15	17	17	11	17	11	13	15
E	8	9	18	12	5	19	21	15	14
S	24	16	20	20	25	18	16	20	20
15 N	13	44	54	37	196	199	193	196	117
NE	7	6	18	10	7	9	14	10	10
NW	1	6	15	7	12	11	7	10	9
Average	7	19	29	18	72	73	71	72	45
25 N	10	42	41	31	35	51	67	51	41
NE	13	11	14	13	5	7	5	6	10
NW	1	5	5	4	14	12	17	14	9
Average	8	19	20	16	18	23	30	24	20
40 N	8	13	14	12	21	15	17	18	15
NE	5	6	7	6	3	5	4	4	5
NW	3	4	2	3	4	3	2	3	3
Average	5	8	8	7	9	8	8	8	8
60 N	6	11	12	10	1	3	2	2	6
NE	5	3	4	4	0	1	0	0	2
NW	3	7	9	6	1	2	0	1	4
Average	5	7	8	7	1	2	1	1	4

16 sq. mm. area, while to the north of the field 408 pollen grains were caught at 5 rods, 117 at 15 rods, 41 at 25 rods, 15 at 40 rods, and 6 at 60 rods. The six pollen grains representing the amount of pollen at 60 rods are approximately one per cent of the number caught in the center of the field. Six is the equivalent of 240 pollen grains per sq. inch or 34,560 per sq. foot (Table 3).

Data were obtained for six days each in 1944 and 1945 (Table 4). On the basis of the daily average for these two years, 513 pollen grains were caught in the center of the field compared with 253 at 5 rods, 61 at 15 rods, 15 at 25 rods, 7 at 40 rods, and 3 at 60 rods to the north of the field. The amount caught at 60 rods from the field was only one-half of one per cent of the amount caught in the center; the daily average number, three, caught at 60 rods is the equivalent of 17,280 pollen grains per sq.

Table 3. Conversion table for calculating the numbers of pollen grains per square inch and per square foot from the number caught per 16 sq. mm. area on exposed microscope slides.

16 sq. mm.	1 sq. in.	1 sq. ft.	16 sq. mm.	1 sq. in.	1 sq. ft.
1	40	5,760	85	3,400	489,600
2	80	11,520	90	3,600	518,400
3	120	17,280	95	3,800	547,200
4	160	23,040	100	4,000	576,000
5	200	28,800	125	5,000	720,000
6	240	34,560	150	6,000	864,000
7	280	40,320	175	7,000	1,008,000
8	320	46,080	200	8,000	1,152,000
9	360	51,840	225	9,000	1,296,000
10	400	57,600	250	10,000	1,440,000
11	440	63,360	275	11,000	1,584,000
12	480	69,120	300	12,000	1,728,000
13	520	74,880	325	13,000	1,872,000
14	560	80,640	350	14,000	2,016,000
15	600	86,400	375	15,000	2,160,000
16	640	92,160	400	16,000	2,304,000
17	680	97,920	425	17,000	2,448,000
18	720	103,680	450	18,000	2,592,000
19	760	109,440	475	19,000	2,736,000
20	800	115,200	500	20,000	2,880,000
21	840	120,960	525	21,000	3,024,000
22	880	126,720	550	22,000	3,168,000
23	920	132,480	575	23,000	3,312,000
24	960	138,240	600	24,000	3,456,000
25	1000	144,000	625	25,000	3,600,000
26	1040	149,760	650	26,000	3,744,000
27	1080	156,520	675	27,000	3,888,000
28	1120	161,280	700	28,000	4,032,000
29	1160	167,040	725	29,000	4,176,000
30	1200	172,800	750	30,000	4,320,000
35	1400	201,600	775	31,000	4,464,000
40	1600	230,400	800	32,000	4,608,000
45	1800	259,200	825	33,000	4,752,000
50	2000	288,000	850	34,000	4,896,000
55	2200	316,800	875	35,000	5,040,000
60	2400	345,600	900	36,000	5,184,000
65	2600	374,400	925	37,000	5,328,000
70	2800	403,200	950	38,000	5,472,000
75	3000	432,000	975	39,000	5,616,000
80	3200	460,800	1000	40,000	5,760,000

foot. Approximately this amount of pollen was shed daily during the pollination cycle, which lasted from eight to ten days. The relative amounts of pollen dispersed in the air at various distances to the north of the field were approximately the same for both years; however, the average daily number caught in 1944 was less than in 1945.

During these two years, when south winds predominated, most of the pollen was dispersed to the north of the field. Lateral dispersal took place in northeasterly and northwesterly directions to distances of 60 rods. Very little pollen was dispersed to the east or west of the field beyond a distance of five rods. Oblique vertical dispersal also occurred as demonstrated by the number of pollen grains caught on slides exposed at the different elevations and distances from the field. At the stations located within five rods of the field, more pollen grains were caught on slides exposed at an elevation of 2.5 feet than at elevations of 5.0 and 10.0 feet (Table 4). At a distance of 15 to 60 rods approximately the same number of grains were caught on the slides exposed at elevations of 2.5, 5.0, and 10.0 feet, regardless of direction. This indicated that as the pollen was blown from the field some vertical dispersion occurred.

Table 4. Average number of pollen grains of bromegrass caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1944 6-day av.				1945 6-day av.				2-year av.
	Elevation (ft.)				Elevation (ft.)				Three
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	elevations
Center	323	216	31	190	1246	1144	115	835	513
5 N	133	101	56	97	499	442	287	409	253
NE	26	15	10	17	5	6	11	7	12
NW	4	3	5	4	53	42	29	41	23
Average	54	40	24	39	186	163	109	152	96
W	5	6	5	5	12	16	21	16	11
E	3	4	5	4	3	12	14	10	7
S	7	4	6	6	17	15	11	14	10
15 N	6	17	18	14	107	110	107	108	61
NE	5	6	8	6	3	4	7	5	6
NW	1	2	5	3	16	21	26	21	12
Average	4	8	10	8	42	45	47	45	26
W	1	1	0	1	12	15	18	15	8
E	8	1	0	3	6	4	6	5	4
25 N	4	2	2	3	17	29	35	27	15
NE	5	5	6	5	3	8	8	6	6
NW	1	2	2	2	11	12	15	13	7
Average	3	3	3	3	10	16	19	15	9
40 N	3	5	5	4	10	8	10	9	7
NE	2	3	4	3	1	2	1	1	2
NW	1	1	3	2	4	2	1	2	2
Average	2	3	4	3	5	4	4	4	4
60 N	2	3	5	3	2	2	1	2	3
NE	3	4	1	3	0	1	0	0	2
NW	1	1	1	1	1	3	0	1	1
Average	2	3	2	2	1	2	0	1	2

Table 5. Average daily number of pollen grains of crested wheatgrass caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1944 5-day av.				1945 5-day av.				2-year av.
	Elevation (ft.)				Elevation (ft.)				Three elevations
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	
Center	716	146	123	418	485	228	81	265	342
5 N	185	192	139	172	61	56	44	54	113
NE	87	74	30	64	12	18	21	17	41
NW	23	22	26	24	93	117	97	102	63
Average	98	96	65	86	55	64	54	58	72
W	19	15	27	20	76	90	81	82	51
E	17	14	12	14	13	14	17	15	15
S	6	3	3	4	....*	....	....	....	....
15 N	41	27	28	32	16	25	20	20	26
NE	15	9	9	11	10	15	17	14	13
NW	7	11	11	10	88	92	85	88	49
Average	21	16	16	18	38	44	41	41	29
E	1	1	3	2	12	9	9	10	6
S	1	0	0	0	....*	....	....	....	....
25 N	4	10	14	9	6	5	15	8	9
NE	8	7	5	7	13	11	15	13	10
NW	6	6	7	6	12	13	20	15	11
Average	6	8	9	7	10	10	17	12	10

* Exposures were not made to the south of the field in 1945.

Crested Wheatgrass. The dispersal of the pollen of crested wheatgrass was studied during a two-year period in a nursery near a residential section. This limited the maximum distances at which slides could be exposed to 25 rods in this trial. Since the period of pollen shedding in crested wheatgrass extends from approximately 2:30 until 6:00 p.m. each day (Fig. 2), the slides were exposed before 1:00 and collected after 8:00 p.m.

An average of data collected during five days is recorded for each year in Table 5. During 1944 the greatest amount of pollen was caught on slides exposed to the north of the field with southerly winds; in 1945 the most pollen was caught to the northwest of the field with winds prevailing from the southeast. The average relative amounts of pollen caught in the direction of greatest concentration were approximately the same. Using the number of pollen grains caught in the center of the field as 100 per cent for each year, only 41.1 per cent as many were caught at five rods and 2.2 per cent at 25 rods in 1944; at these respective distances in 1945, 39.0 per cent and 6.0 per cent were caught.

On the basis of the two-year average, only 11 pollen grains (3.2 per cent) of the 342 caught in the center of the field were caught at a distance of 25 rods. This indicates that the concentration of the pollen in the air had been drastically reduced, yet the quantity present at 25 rods would be sufficient to be a factor in effecting cross-pollination at that distance. Eleven pollen grains is the equivalent of 440 per sq. inch, or 63,360 per sq. foot (Table 3).

The dispersal of the pollen followed the same trend as that discussed for bromegrass. The greatest amount of pollen was caught on the slides exposed in the direction opposite the prevailing wind, with smaller amounts being caught on slides exposed to each side. A few pollen grains were caught on slides exposed to the south of the field at five rods. Only one grain per 16 sq. mm. area was caught at 15 rods, and the slides were free of pollen at 25 rods in this direction. This indicates that southerly winds prevailed throughout the 1944 pollination season. As a result, slides were not exposed to the south of the field in 1945, except at one station which served as a check.

Intermediate Wheatgrass. The distance of dispersal of the pollen of intermediate wheatgrass was investigated during the 1944 and 1945 pollination seasons. A small breeding nursery was surrounded with stations to a distance of 25 rods in the directions to the north of the field. In 1944 some pollen was caught on slides exposed at stations to the east and west of the field, at distances of 5 and 15 rods (Tables 6 and 7). No pollen was caught on slides exposed at any stations to the south. As a result, exposures at these stations were discontinued in 1945. The daily period of pollen shedding in this grass extended from approximately 2:30 until 5:00 p.m. (Fig. 2). The slides were exposed before 1:00 and collected after 8:00 p.m.

Data obtained on the day of maximum pollen shedding each year are recorded in Table 6. A southwest wind in 1944 resulted in a heavy pollen catch on the slides exposed on the northeast and north sides of the field; in 1945 a southeast wind blew the greatest proportion of the pollen to the northwest, north and west of the field.

Table 6. Number of pollen grains of intermediate wheatgrass caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field on the day of maximum pollination. Southeast wind 6 mph., July 1, 1944. Southeast wind 5 mph., July 2, 1945.

Distance (rods) and direction from the field	1944				1945				2-year av.
	Elevation (ft.)				Elevation (ft.)				Three
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	elevations
Center	529	336	45	303	243	143	62	149	226
5 N	48	44	37	43	93	53	31	59	51
NE	105	105	36	83	16	15	11	14	49
NW	10	4	6	7	76	62	51	63	35
Average	55	51	26	44	62	43	31	45	45
W	2	2	0	1	67	41	22	43	22
E	5	4	2	4	20	12	9	14	9
15 N	12	13	9	11	16	19	13	16	14
NE	6	0	4	4	7	12	12	10	7
NW	5	1	4	3	30	39	36	35	19
Average	8	5	6	6	18	23	20	20	13
E	0	0	1	0	12	15	15	14	7
25 N	7	7	13	9	6	4	7	6	7
NE	0	0	0	0	10	4	6	7	3
NW	3	2	2	2	15	14	19	14	9
Average	3	3	5	4	10	7	11	9	7

Table 7. Average daily number of pollen grains of intermediate wheatgrass caught on 16 sq. mm. areas of microsope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1944 9-day av. Elevation (ft.)				1945 4-day av. Elevation (ft.)				2-year av. Three elevations
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	
Center	248	129	25	134	255	139	42	146	140
5 N	21	20	17	19	46	31	20	32	26
NE	17	17	7	14	16	18	17	17	16
NW	15	9	4	9	38	32	24	31	20
Average	18	15	9	14	33	27	20	27	21
W	1	1	0	1	37	25	15	26	14
E	1	1	0	1	11	11	8	10	6
15 N	4	4	3	4	14	14	10	13	9
NE	1	0	1	1	7	16	17	13	7
NW	3	2	2	2	15	14	13	14	8
Average	3	2	2	2	12	15	13	13	8
E	0	0	0	0	8	8	7	8	4
25 N	2	2	3	2	5	5	6	5	4
NE	0	0	1	0	5	5	4	5	3
NW	1	1	1	1	6	5	6	6	4
Average	1	1	2	1	5	5	5	5	3

The nine-day average for 1944 and the four-day average for 1945 are recorded in Table 7. The average daily amounts of pollen caught on the slides were about the same in both years. On the basis of the two-year average, there were 140 pollen grains caught in the center of the field, whereas to the north side, 26 were caught at five rods and four at 25 rods. Four are 2.8 per cent of the amount caught at the field source. The average daily number, four, is the equivalent of 23,040 per sq. ft., (Table 3), an amount large enough to cause serious contamination.

Buffalograss. The distance of dispersal of the pollen of buffalograss was investigated for a five-day period in 1945 (Table 8). Slides were exposed daily in the afternoon to a distance of 40 rods from the field in northerly directions to catch the pollen that was shed the following morning. The daily pollen-shedding period of buffalograss occurred from 6:00 a.m. until 12:00 noon (Fig. 5).

Buffalograss is the shortest plant of the grasses studied. The spikes were produced three to eight inches above the ground. In addition to the exposures that were made at elevations of 2.5, 5.0, and 10.0 feet, exposures were replicated four times over the field at elevations of 0, 6, 9, and 15 inches.

The greatest number of pollen grains (654) was caught on slides exposed in the center of the field at an elevation of six inches or the average height of the spikes. Slides that were placed on the ground caught an average of 365 pollen grains per unit area (footnote Table 8). These figures indicate that a very large percentage of the pollen fell directly to the ground. The average number of pollen grains caught during the five days at the higher elevations was 293 at 9 inches, 189 at 15 inches, 90 at 2.5 feet, 38 at 5.0 feet, and 14 at 10.0 feet. Only 2.1 per cent

Table 8. Number of pollen grains of buffalograss caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1945 Five-day average			
	Elevation (feet)			
	2.5	5.0	10.0	average
Center *	90	38	14	47
5 N	73	28	15	39
NE	26	25	18	23
NW	27	23	9	20
Average	42	25	14	27
15 N	10	9	6	8
NE	12	18	11	14
NW	15	11	7	11
Average	12	13	8	11
25 N	5	5	3	4
NE	7	12	7	9
NW	4	6	5	5
Average	5	8	5	6
40 N	3	2	3	3

Table 9. Average daily number of pollen grains of switchgrass caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1944 6-day av.				1945 4-day av.				2-year av.
	Elevation (ft.)				Elevation (ft.)				Three elevations
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	
Center	280	402	116	266	154	279	129	187	226
5 N	41	68	56	55	29	75	62	55	55
NE	4	7	5	5	10	12	10	11	8
NW	18	33	31	27	6	7	6	6	17
Average	21	36	31	29	15	31	26	24	27
E	1	2	1	1	4	3	3	3	2
15 N	12	20	16	16	15	20	21	19	18
NE	2	2	2	2	5	7	4	5	3
NW	1	2	3	2	3	4	4	4	3
Average	5	8	7	7	8	10	10	9	8
W	1	0	1	1	2	4	2	3	2
E	0	0	0	0	1	2	2	2	1
20 N	6	4	4	5	5	7	6	6	5
NE	2	1	1	1	3	4	3	3	2
NW	1	1	1	1	1	1	1	1	1
Average	3	2	2	2	3	4	3	3	3
40 N	1	1	2	1	1	3	2	2	2
NE	0	0	0	0	2	1	1	1	1
NW	0	0	1	0	1	0	1	1	1
Average	1	1	1	1	1	1	1	1	1
60 N	0	1	1	1	1	1	1	1	1

* Exposures were replicated four times at elevations of 0, 6, 9, and 15 inches in the center of the field with the following average numbers of pollen grains caught per 16 sq. mm. area; 365, 654, 293, and 189, respectively.

as many pollen grains were caught in the center of the field at an elevation of 10.0 feet as were caught at an elevation of six inches.

Based on the average of the three regular elevations for the five-day period, 47 pollen grains were caught in the center of the field, while only three were caught at 40 rods to the north.

Switchgrass. The dispersal of the pollen of switchgrass was studied for two years, with the slides being exposed mostly in northerly directions from the field (Table 9).

The period of pollen shedding extended from 10:00 a.m. until 2:30 p.m. (Fig. 7). The slides were exposed daily from 9:00 a.m. until 4:00 p.m. The slides were contaminated with pollen from *Kochia,* giant ragweed, rough pigweed, and hemp, but it was never difficult to obtain accurate counts of the switchgrass pollen.

As a two-year average, 226 pollen grains were caught per unit area of microscope slide at the center of the field; to the north, 55 were caught at 5 rods, 18 at 15 rods, five at 25 rods, two at 40 rods, and one at 60 rods. One pollen grain is only 0.4 of one per cent of the amount caught in the center of the field, yet it is the equivalent of 5,760 pollen grains per square foot. The greatest number of pollen grains were caught on slides exposed at an elevation of 5.0 feet or the average level of the grass panicles.

Rye. The dispersal of rye pollen was studied during the two-year period. The distance of exposure of slides was limited to 25 rods in 1944, but in 1945 slides were exposed at distances up to 80 rods. The period of pollen shedding extended from about 3:00 until 11:00 a.m. each day (Fig. 4). Slides were exposed about 4:00 p.m. and left until the same time the following day when new exposures were made.

The average data for a nine-day period in 1944 and a four-day period in 1945 are presented in Table 10. On the basis of the two-year average, 640 pollen grains were caught in the center of the field, while to the north of the field 264 were caught at 5 rods, 123 at 15 rods, and 64 at 25 rods. Using the number of pollen grains caught each year on slides exposed in the center of the field as 100 per cent, then in 1944 only 54.4 per cent as many were caught at 5 rods and 1.0 per cent at 25 rods. In 1945 at these respective distances, 53.3 per cent and 10.5 per cent were

Table 10. Average daily number of pollen grains of rye caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field	1944 9-day av. Elevation (ft.)				1945 4 day av. Elevation (ft.)				2-year av. Three elevations
	2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	
Center	283	176	123	194	782	1389	1085	1085	640
5 N	65	96	62	74	433	520	407	453	264
NE	63	66	46	58	12	10	11	11	35
NW	30	29	50	36	7	6	7	7	22
Average	53	64	53	57	151	178	142	157	107
15 N	14	10	18	14	229	251	216	232	123
25 N	2	3	6	4	136	122	114	124	64
40 N	..	..	..	..	55	50	51	52	....
60 N	..	..	..	..	10	11	12	11	....
80 N	..	..	..	..	6	6	5	6	....

caught. This amount was decreased to 1.9 per cent at 60 rods and 1.2 per cent at 80 rods. Extremely heavy pollen shedding and strong winds prevailed throughout the four-day period on which data were obtained in 1945, which may account for the greater amount of pollen than in 1944 dispersed in the air at 15 and 25 rods.

Corn. The distance of dispersal of corn pollen is a subject of much discussion. The effect of foreign pollen on endosperm characters (xenia) has been given more attention in corn than in the other grasses. The isolation used in commercial corn production has been based on distances sufficient to reduce crossing to a practical minimum.

An investigation was conducted on the dispersal of corn pollen for two years, with slides being exposed mostly to the north of the field (Table 11). The slides were exposed daily in late afternoon. Pollen shedding extended from approximately 7:00 a.m. until 4:00 p.m. (Fig. 8).

Data based on the average of all elevations for the two-year period show 203 pollen grains were caught daily in the center of the field, while to the north 35 were caught at 5 rods, nine at 15 rods, six at 25 rods,

Table 11. Average daily number of pollen grains of corn caught on 16 sq. mm. areas of microscope slides exposed at various elevations and distances from the field during pollination.

Distance (rods) and direction from the field		1944 5 day av. Elevation (ft.)				1945 4-day av. Elevation (ft.)				2-year av. Three elevations
		2.5	5.0	10.0	av.	2.5	5.0	10.0	av.	
Center		139	265	158	187	164	293	198	218	203
5	N	18	20	23	20	46	42	59	49	35
	NE	5	5	3	4	7	5	5	6	5
	NW	9	10	8	9	18	13	19	17	13
Average		11	12	11	11	24	20	28	24	18
	W	12	14	14	14	14	12	14	13	13
	E	0	1	1	1	4	2	3	3	2
15	N	4	3	2	3	17	14	14	15	9
	NE	2	1	2	2	2	3	3	3	3
	NW	3	1	2	2	6	5	8	6	4
Average		3	2	2	2	8	7	8	8	5
	W	1	3	2	2	4	5	3	4	3
	E	0	1	0	0	0	1	0	0	0
25	N	2	1	2	2	12	9	8	10	6
	NE	2	1	2	2	2	3	1	2	2
	NW	1	2	2	2	6	5	4	5	4
Average		2	1	2	2	7	6	4	6	4
40	N	1	1	1	1	3	2	1	2	2
	NE	1	1	1	1	2	1	1	1	1
	NW	1	1	1	1	2	3	2	2	2
Average		1	1	1	1	2	2	1	2	1
60	N	1	1	1	1	2	1	1	1	1
	NE	0	1	1	1	1	1	1	1	1
	NW	0	0	0	0	1	2	1	1	1
Average		0	1	1	1	1	1	1	1	1

two at 40 rods, and one at 60 rods. The average of one pollen grain caught at 60 rods is the equivalent of 40 per sq. inch or 5,760 per sq. foot (Table 4).

Considering this in another light, there are approximately three square inches of silk mass exposed per shoot. On the basis of data obtained from exposed slides, about 120 grains would have fallen on the silk area daily in fields at a distance of 60 rods. Over a 10- to 12-day period of pollination, 1,200 to 1,440 pollen grains would have fallen on the area occupied by the silks of one ear shoot, or per 800 to 1,000 ovules. With no competition this amount would be sufficient to cause fair seed set.

Viability of Pollen

The amount of pollen dispersed in the air at various distances from the source was determined. It seemed desirable to ascertain if all or any part of this pollen is viable, in order to estimate the amount of contamination that might be expected under such conditions. In 1944, studies were made on the amount of fertilization effected by pollen of buffalograss and corn which had been stored under different treatments. In addition, in 1945, a study was made as to the amount of fertilization effected in corn by pollen which had been blown through the air for 50 rods.

Buffalograss pollen was studied under two conditions of storage. In Treatment 1, it was stored under a temperature of 113° F. and a relative humidity of 30 per cent, while in Treatment 2 it was stored under a temperature of 77° F. and a relative humidity of 40 per cent. After periods of 24 and 48 hours of storage, pollinations were made on the bagged inflorescences of three plants. Compared with the checks, which set no seed, 25 per cent of the ovules that were pollinated with pollen from Treatment 1, and 35 per cent from Treatment 2 set seed after 24 hours of such storage. No seed was set in either case after 48 hours of storage.

The longevity of corn pollen was studied under field conditions at the time of pollination. Pollen was collected in pollinating bags at 8:50 a.m. on July 19, 1944. Part of the bags were placed on the ground in direct sunlight at a temperature of 96° F. The remaining bags were placed on the ground in the shade of the corn plants where the temperature was approximately 86° F. Pollinations of three ear shoots with pollen from each treatment were made at three-hour intervals, beginning at 9:00 a.m. All silks used in this study were at a receptive age and had been covered since the date of emergence.

The average seed set per ear obtained from the pollen stored in direct sunlight was 600 kernels at the beginning of the period, 575 after three hours, and zero after six hours. The average seed set per ear obtained from the pollen stored in the shade was 600 kernels at the beginning of the period, 492 after three hours, 357 after 12 hours, 323 after 27 hours, 66 after 30 hours, and zero after 33 hours.

The data obtained from these studies indicate that a large amount of the pollen remained viable for several hours under these conditions. If it is assumed that pollen travels approximately as fast as the wind, under a wind velocity of nine mph. it would require only 1.67 minutes for pollen to travel 80 rods. Based on this assumption, it appears probable that most of the pollen remains viable at this distance under field conditions.

In 1945, several isolated stalks of corn were growing 50 rods to the north of a field. These plants were detasseled before the field of corn began to shed pollen. After two days of pollen dispersal by south winds, it was shown that 7.2 per cent of the ovules had set seed. On this basis, about 40 per cent of the ovules might have been outcrossed and set seed, if free of competition throughout a pollination cycle of 12 days. This amount of cross-fertilization is sufficient to cause the loss of genetic identity.

Amounts of Pollen at Various Distances

The pollen dispersal of seven species of forage grasses and cereal crops of the cross-pollinated group was studied during 1944 and 1945. The average number of pollen grains caught per square foot at various distances from the field was determined for each grass. The calculations were made from the pollen counts of slides exposed in the direction of greatest concentration of pollen on the day of maximum pollen shedding. The average number of pollen grains caught at the two elevations nearest the height of the inflorescence of each grass was used as the reading for each station. These data are summarized in Table 12. Calculated

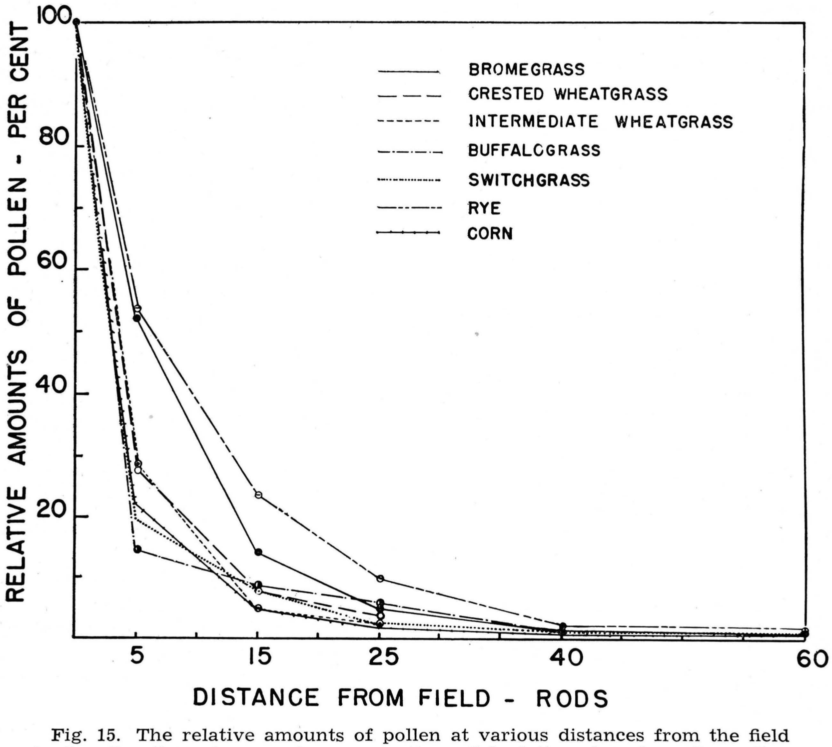

Fig. 15. The relative amounts of pollen at various distances from the field in the direction of greatest concentration. Calculations based on the pollen dissemination during day of maximum pollen shedding in each of two years.

Table 12. Calculated numbers of pollen grains per square foot disseminated to different distances during a day of active pollination. Numbers based on pollen counts from stations in the direction of greatest concentration on the day of maximum pollen shedding in each of two years.

Grasses	Distance from field—Rods				
	5	15	25	40	60
	Thousands	Thousands	Thousands	Thousands	Thousands
Bromegrass	2,673	710	242	92	40
Crested wheatgrass	1,313	357	167	....	....
Intermediate wheatgrass	518	86	43	....	....
Buffalograss	392	230	144	26	....
Switchgrass	403	150	49	20	9
Rye	5,507	2,413	1,066	184	121
Corn	357	69	32	10	7

numbers of pollen grains disseminated daily at distances up to 25 rods are extremely large, whereas the numbers at 40 and 60 rods are sufficient to be important factors in effecting fertilization.

These data are presented in graphic form in Figure 15, which gives the relative amounts of pollen of the different grasses (in per cent) caught at the various distances from the field. The same general trend of dispersal was found in all of these grasses. Using the average amount of pollen caught in the center of the field for all of the grasses studied as 100 per cent, approximately 31.0 per cent was caught per unit area at 5 rods, 10.0 per cent at 15 rods, 4.4 per cent at 25 rods, 1.2 per cent at 40 rods, 0.8 per cent at 60 rods to the north. However, the low percentage of pollen, representing several thousand pollen grains per square foot, caught at 60 rods must be considered an omnipresent source of contamination in the field production of pure seed stocks.

Discussion

THE FOREGOING EXPERIMENTS indicate that the dispersal of the pollen of the different grasses followed approximately the same general trend. For the two-year period, 1944 and 1945, south winds predominated during most of the seasonal pollination cycle for each grass studied. Pollen dispersal studies were made only on these days. Accordingly, the larger amounts of pollen were caught on the exposures made to the north of the field with less pollen being caught in other directions. Since it may be assumed that pollen would be dispersed similarly in other directions, because of changes in wind, it would seem advisable to isolate seed fields the same distance in different directions.

Striking differences in the amounts of pollen produced by the grasses were shown. Rye and bromegrass produced larger amounts of pollen than other grasses studied. A somewhat larger proportion of pollen of these grasses was disseminated to distances of 5 and 15 rods than for the other grasses; however, the relative amounts of pollen caught at 60 rods for each of the grasses, compared with the amounts caught in the center of the field, were about the same. With gravity acting on the pollen, and with dispersion occurring as it is blown from the source, a rapid decrease occurs in the pollen load.

On the basis of the data obtained in these investigations, it appears that at 25 rods from the field considerable quantities of pollen remain dispersed in the air. Not until 40 rods is reached is the amount reduced to relatively small quantities. At 60 rods the amount is further reduced to about one per cent of that caught at the field source. One per cent of pollen is the equivalent of several thousand pollen grains per square foot, which would be sufficient to effect much fertilization in the absence of competition. When this pollen is considered as a contaminant, the odds are approximately 100 to 1 in favor of a field's own pollen. However, these odds would be drastically reduced within selections of certain grasses in which partial sib-sterility or self-sterility exists, or in which a differential rate of pollen-tube growth occurs. The data from these investigations suggest that the chances of maintaining genetic identity are much greater when seed is produced under an isolation of 60 rods or greater as compared with 25 or 40 rods.

With milo (20), in which as little as six per cent cross-pollination may occur in adjoining rows under natural conditions, 40 and 60 rods are required as the minimum isolation for the production of certified and foundation seed, respectively, in most official seed certification programs. The effects of cross-pollination in many of the sorghums is visible in the resultant seed and crop. The phenomena of xenia and hybrid vigor have been instrumental in setting the isolation requirements at the distances above indicated. It appears that with certain perennial grasses, where a much higher percentage of cross-pollination is recognized, the isolation distances should be as great or greater than those for sorghum in order to insure the maintenance of genetic identity.

Since the breeding of these forage grasses is in its infancy, no critical work has yet been done with genetic testers to determine the extent of such cross-pollination. Until such critical work has been done, it would seem desirable to base the isolation requirements on information obtained from studies of pollen load in the air.

Summary

STUDIES were conducted to ascertain the time of day and the number of days that certain grasses bloom and shed pollen, and the distances to which the pollen of grasses is dispersed by the wind in amounts sufficient to cause contamination in seed-stock fields by way of outcrossing. To obtain data on these aspects of pollination and seed production, approximately 7,500 vaseline-coated microscope slides were so exposed during 1944 and 1945 as to intercept air-borne pollen.

A total of 16 cool-season and 13 warm-season grasses were studied to determine the time of day in which pollen shedding took place. Of these 29 grasses, 13 were investigated by means of slide exposures. In addition, observations were made on 16 other grasses.

When the meteorological conditions were optimum for blooming, the daily pollination periods occurred rather regularly at the same time of day for each grass throughout its seasonal pollination cycle.

In the cool-season group, the daily pollination of rye, timothy, and Kentucky bluegrass was found to occur in the morning, while for the remaining grasses of this group it occurred in the afternoon. In all of the warm-season grasses studied, the daily pollination period was found to begin in the forenoon.

With most of the grasses, two to six hours in each of several successive or intermittent days were required for the completion of blooming and pollen shedding, although with rye, sorghum, and corn, daily periods of eight to nine hours were common.

To determine the number of days of pollen dispersal, four grasses were studied by the use of pollen-intercepting slides, and 25 others were also observed. With single inflorescence of most of these grasses, the cycle of pollen dispersal continued for seven or eight days, with four and twelve days being the extremes. The pollen dispersal by a given plant or a field of plants extends over a longer period than that of a single inflorescence.

When a grass reaches the blooming stage, the time of actual blooming and shedding of pollen may be greatly delayed or even inhibited by unfavorable atmospheric conditions. Temperature is the most important external factor affecting the time of pollination in grasses. The optimum temperature for blooming varies for different species. It was found that for each grass studied there is a minimum temperature below which blooming is delayed for hours or even days.

The daily pollination periods occurred partially or entirely during periods of darkness with 13 of the grasses studied. Others normally shed pollen in daylight. Wind movement was important in speeding up anthesis, dehiscence, and pollen dispersal. High relative humidity was found to delay dehiscence of anthers and dispersal of pollen with two grasses.

Observations made during these investigations show that the time of day of blooming of grass florets is the result of an interaction of inherent and external factors. When florets have reached the blooming stage the exact time of blooming is determined by the existing meteorological conditions.

Alternation of days of light and heavy pollen shedding occurred more frequently in the cool-season than in the warm-season grasses. Low temperatures reduced the number of florets that bloomed. However, on the following day a greater number of florets had grown to maturity during this delayed period, which resulted in heavy blooming and a larger number of pollen grains being caught.

The amount and distance of pollen dispersal under field conditions were studied for seven species of cross-pollinated forage grasses and cereal crops by means of suitably exposed microscope slides during two years.

The dispersal of the pollen of all the grasses followed approximately the same general trend. With prevailing southerly winds, most of the pollen was dispersed toward the north from the fields under study. Some lateral dispersal took place in northeasterly and northwesterly directions. Dispersal in other directions was extremely light. Although no data were recorded of the pollen dispersal on days with other wind directions, all wind directions should be considered in setting up isolation requirements.

With gravity acting on the pollen and with dispersion occurring as it is blown from the field, a rapid decrease occurred in the pollen load. Using the average amount of pollen caught in the center of the field for all of the grasses studied as 100 per cent, approximately 31.0 per cent was caught per unit area at 5 rods, 10.0 per cent at 15 rods, 4.4 per cent at 25 rods, 1.2 per cent at 40 rods, and 0.8 per cent at 60 rods to the north. However, these low percentages usually represent a considerable number of pollen grains.

The chances of maintaining genetic identity of improved strains of cross-pollinated grasses are much greater when seed is produced under an isolation of 60 rods or more than at lesser distances. Even the relatively low percentages of total pollen caught at 60 rods must be considered an omnipresent source of contamination in the field production of pure seed stocks.

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